ERRATA ET CORRIGENDA

P. 514 :   line 7, for ' anterior ' read ' posterior '.

P. 522 :   legend of Fig. 540, insert ' d, ductus caroticus '.

P. 588 :   line 3 from bottom, for ' 849 ' read ' 949 '.

P. 592 :   legend of Fig. 600, insert ' sa, sinus endolymphaticus '.

P. 593 :   line 19, insert before ' Evans ', ' Delaroche, Dufossé '.

P. 597 :   line 18 from bottom, insert ' Baglioni, Latter ' before ' Dakin '.

P. 605 :   line 1 for ' contributes ' read ' contribute '.

P. 617 :   legend of Fig. 619, and p. 619 legend of Fig. 621, insert ' plc, splanchnocoele '.

P. 629 :   legend of Fig. 630, throughout for ' right ' read ' left '.

P. 658 :   legend of Fig. 655, insert ' sc, splanchnocoele '.

P. 659 :   line 3 from top, for ' Fig. 665 ' read ' Fig. 655 '.

P. 683 :   legend of Fig. 680, for ' cardinal view ' read ' cardinal vein '.

P. 722 :   line 4 from bottom, for ' Fig. 747 ' read ' Figs. 745 and 750 '.

P. 750 :   line 2 from bottom, for ' ophthalmicus ' read ' ophthalmica '.

P. 774 :   legend of Fig. 748, $cn.$, for ' iris ' read ' dilatator iridis '; for ' n, motor fibres ' read ' somatic motor fibres '; $nc.$, for ' to iris ' read ' to sphincter iridis '.

P. 795 :   line 14 from bottom, for ' Geol. Mag. ; . 1914 ' read ' Anat. Anz. v. 44, 1913 '.

P. 819 :   reference No. 933, for ' Reiss ' read ' Reis '.

P. 837 :   in Index, insert ' Weber's apparatus, 590, 599 f., 600 f.'.

CHAPTER IX

VISCERAL CLEFTS AND GILLS

THE VISCERAL CLEFTS AND GILLS

OF all the characteristic features of the vertebrate phylum few are more fundamental than the gill-slits. Serving primarily for the passage of a respiratory and nutritive current of water from the pharynx to the exterior, they occur not only in the Cephalochorda, Cyclostomata, and Pisces, but also in Amphibia, and in a more or less reduced condition in the embryonic stages of all Amniota. Moreover, their presence in Tunicata, Enteropneusta, and Pterobranchia is evidence that gill-slits were possessed by the common ancestor of all these groups.

The structure of the gills of *Amphioxus* is so well known that it need not here be described in detail; suffice it to say that each primary slit is subdivided by a tongue bar into two secondary slits and these again by delicate synapticula, and that the whole sieve-like structure is supported by an internal chitinoid cuticular skeleton [1] (Willey, 94; Benham, 1893; Boveri, 814). The atrium into which the gill-slits open arises as a ventral invagination of the ectoderm (Lankester and Willey, 792), and has probably been derived phylogenetically from paired

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[1] The gills of the Enteropneusta so closely resemble those of Amphioxus that, in spite of Spengel's objections (1893), we seem justified in supposing that in many respects they are strictly homologous (tongue-bars, synapticula, etc.). In a general way the atrium of Amphioxus, of Tunicata, and the outer gill-chambers of Enteropneusta correspond.

longitudinal grooves joining the external gill-apertures. Although the gill-slits of *Amphioxus* are no doubt respiratory, yet their great development and large number are probably specialisations related to another function, namely, the creating by means of their cilia and sifting of a current of water carrying food particles which are caught in mucus secreted by the endostyle. The food material so entangled is driven upwards along the peripharyngeal ciliated grooves and obliquely over the inner surface of the gill-bars to the dorsal groove, whence it passes backwards to the intestine (Orton, 796). In aquatic Craniata the respiratory function is dominant and the gill-bars become provided with thin-walled lamellae ; but even in them gill-rakers are generally present along their inner edges which serve to prevent food from passing out of the pharynx, and in some fishes the bars may be armed with teeth which help in mastication, Fig. 599.

The gill-slits develop by the meeting of paired outgrowths of the endodermal wall of the pharynx with the outer ectoderm, and the piercing of the thin membrane so formed, Figs. 514, 517. Usually corresponding shallower ectodermal ingrowths meet the pharyngeal pouches. When the membrane is pierced the limit between ectoderm and endoderm soon becomes obscured and lost. The gill-slits develop from before backwards, and their number is increased or decreased at the end of the series (though the first pair may be closed, see below, p. 519), and behind the open slits there are usually to be found some incompletely developed owing to the failure of the pouch to reach the ectoderm, or of the closing membrane to become pierced. Speaking quite generally, the number of gill-slits is larger in the lower than in the higher vertebrates. But if we ask how many were present in the ancestral Vertebrate, no definite answer can yet be given. The very large number of slits seen in *Amphioxus*, some 180 pairs in the adult, can hardly be truly primitive. The whole pharynx and its slits have probably been greatly extended in adaptation to the mode of feeding by ciliary action ; indeed, new slits seem to be added throughout life, or at all events so long as the animal continues to grow. Nevertheless, it is probable that the slits were originally more numerous than in modern Pisces, in which there are never more than eight and usually only six pairs of visceral clefts.[1] For in the Cyclostomes, where the first cleft is obliterated in ontogeny (Dohrn, 333, 780 ;

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[1] In Amphioxus the first gill-slit is closed in development (Willey, 94). The first slit in Craniata is always modified, and usually closed, but may remain as an open spiracle in some Pisces ; it corresponds to the facial nerve, is situated between the mandibular and the hyoid arches, and usually goes by the name of spiracular slit or pouch (p. 519). The more posterior truly respiratory slits are called branchial.

Dean, 778), there may remain as many as 14 pairs of open branchial slits: 7 in Petromyzontia, 6 (and an oesophageal duct) in *Myxine*, and
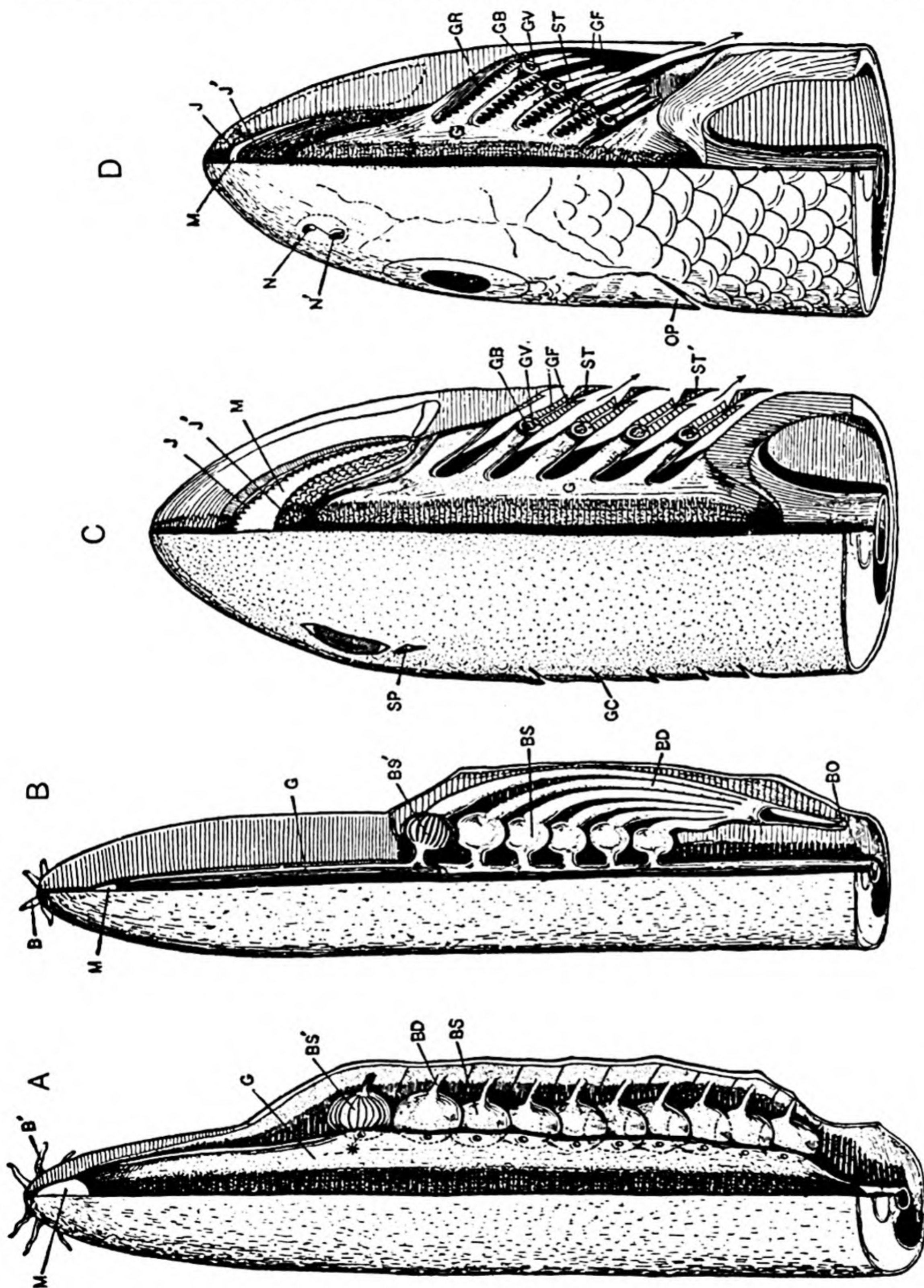

FIG. 513.

Diagrams of head of: A, *Bdellostoma*; B, *Myxine*; C, a *Selachian*; D, a *Teleost*. Dorsal view partly dissected to show arrangement of gills. (From B. Dean, *Fishes Living and Fossil*, 1895.) B, Barbels; *BD*, outer duct from gill-pouch; *BO*, common opening of branchial ducts; *BS*, gill-sac; *BS'*, gill-sac opened; *G*, gullet; *GB*, skeletal branchial arch; *GF*, gill-lamella; *GR*, gill-raker; *GV*, branchial vessel; *J, J'*, upper and lower jaws; *M*, mouth; *N, N'*, anterior and posterior nostrils; *OP*, operculum; *SP*, spiracle; *ST*, *ST'*, intertrematic gill-septum; *, inner branchial opening; →, direction of water current.

6 to 14 (and a duct) in *Bdellostoma*, Figs. 518-19. In the majority of Pisces there are 5 pairs of branchial slits; but among Selachians there may be more (6 in *Hexanchus* and *Chlamydoselache*, 7 in *Heptanchus*, 6 in

Pliotrema, an aberrant Pristiophorid (Regan, 798)). The earliest known fossil fish, the Ostracodermi, appear to have usually possessed not more than ten pairs of slits. Traces of a posterior vestigial slit or visceral arch have been described in Selachii by various authors (Hawkes, 689, Daniel, 674, in *Heterodontus*; Goodey, 685, Braus, 673, K. Fürbringer, 681, in Notidanids, etc.). Moreover, the suprapericardial body (ultimobranchial body) is considered to have been derived from a vestigial pouch behind the last branchial slit. In the Tetrapoda, also, four or five visceral pouches are usually developed behind the spiracular (5 in Amphibia, 4 in Aves, 5 in Mammalia). A posterior vestigial sixth pair has been described
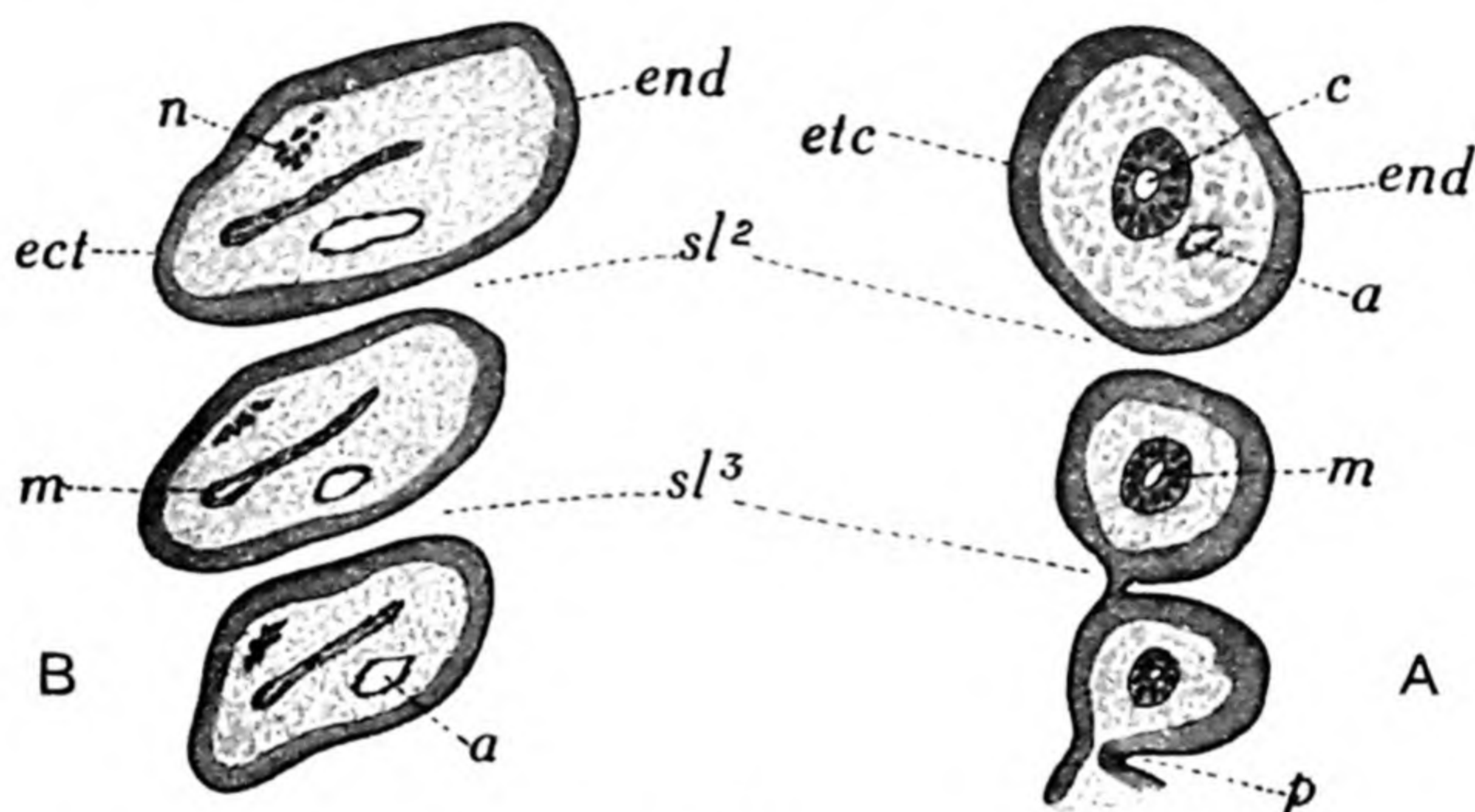

FIG. 514.

Horizontal sections through wall of pharynx of embryo *Scyllium canicula*, cutting gill-bars transversely. A, Stage I; B, stage K. *a*, Vascular arch; *c*, coelomic canal; *ect* and *etc*, ectoderm on outer surface; *end*, endoderm on inner surface; *m*, tube of lateral plate mesoderm in A, giving rise to flattened muscular plate in B; *n*, post-trematic nerve; *p*, endodermal gill-pouch; *sl*, gill-slit.

in Urodela, and even a seventh in Apoda (Marcus, 752). We may conclude that the original number of slits in the ancestral Gnathostome was not very large, possibly only seven or eight including the spiracular.

Whether the gill-slits were originally segmental is an interesting question. In no adult Vertebrate does branchiomerism correspond strictly with the metamerism of the body as indicated by the myotomes. When in the embryo an endodermal gill-pouch grows outwards it meets and pierces the lateral plate mesoderm to reach the ectoderm (p. 487), and since the primary segmentation has already disappeared in this plate, the exact relation the pouch may have borne to the mesoblastic segments is obscured. Nevertheless, it is probable that they were originally intersegmental in position. At their first appearance the first few pouches alternate with the segmental somites above them; but, owing to differential growth, the great enlargement of the gill-pouches and arches, and their tendency to spread backwards, any such original correspondence

is soon lost, especially in Gnathostomes. Strong evidence that the visceral clefts were originally intersegmental is afforded by the nerves ; for behind each passes the main branch of one segmental (really intersegmental) dorsal-root nerve in regular sequence (see p. 219). This is particularly striking in the larval *Amphioxus* (Goodrich, 1909) and in *Petromyzon*.
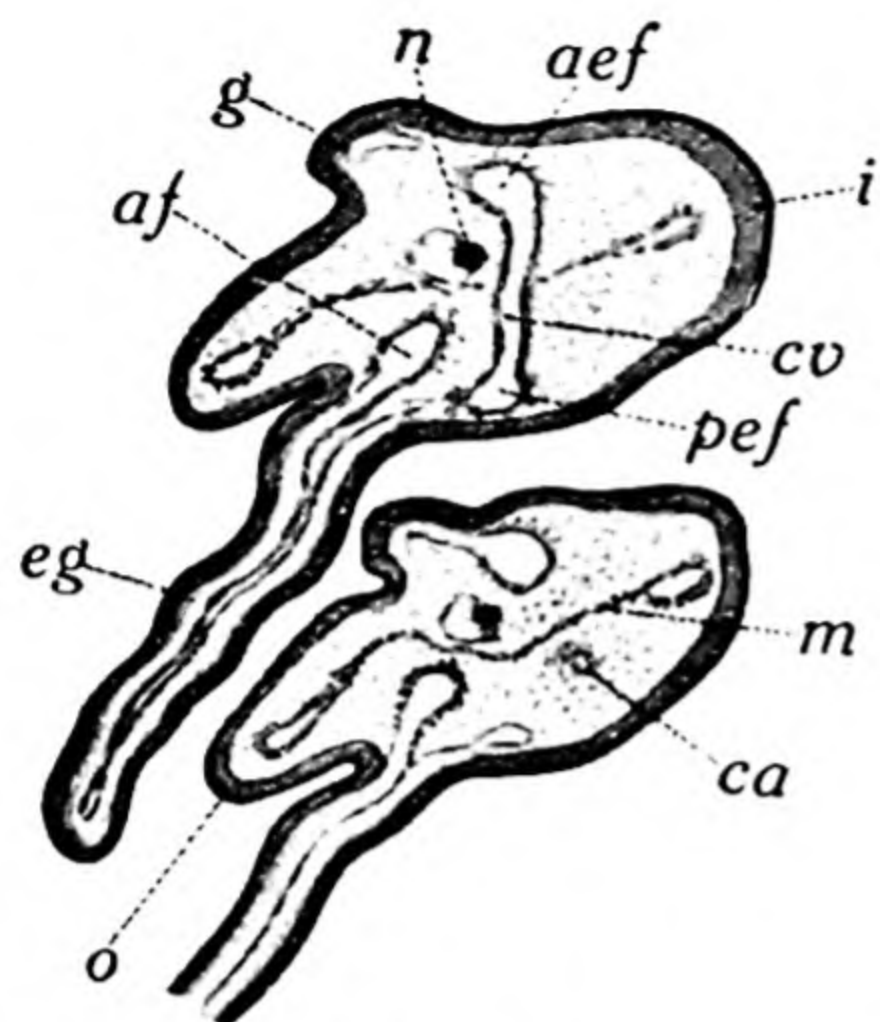

FIG. 515.

Scyllium canicula, embryo 32 mm. long ; portion of horizontal section through wall of pharynx showing two branchial arches cut transversely. *af*, Afferent vessel ; *aef*, *pef*, anterior and posterior efferent vessels ; *ca*, mesenchymatous rudiment of skeletal arch ; *cv*, cross commissural vessel ; *eg*, external gill-filament ; *g*, anterior gill-lamella ; *i*, inner endodermal surface ; *n*, posttrematic nerve ; *o*, outer ectodermal surface.

Leaving aside for the present the specialised spiracular slit, we find that the branchial clefts are separated from each other by branchial bars (gill-arches), covered by ectoderm on their outer and endoderm on their inner surface, and containing lateral plate mesoderm with a coelomic cavity. This cavity, the remains of the coelom of the lateral plate in this region, persists in *Amphioxus*, Fig. 707, but is soon obliterated in the embryonic stages of Craniata, Figs. 514, 517. From its walls, however, develop branchial muscles (p. 219). In the aquatic gill-bearing Gnathostomes the large branchial pouches are compressed and open into the pharynx by dorso-ventrally elongated slits. The intervening bars are differentiated into an inner region containing the skeletal arch, and an outer region or septum passing obliquely backwards towards the surface, containing nerves and blood-vessels and bearing the respiratory lamellae. Primitively, no doubt, the visceral clefts all opened separately to the exterior as they still do in modern Selachii, Fig. 513.

The respiratory lamellae of Pisces are typically thin folds extending from the gill-septum, and set transversely to the axis of the gill-bar, Figs 515-17. They bear on their upper and under surfaces numerous
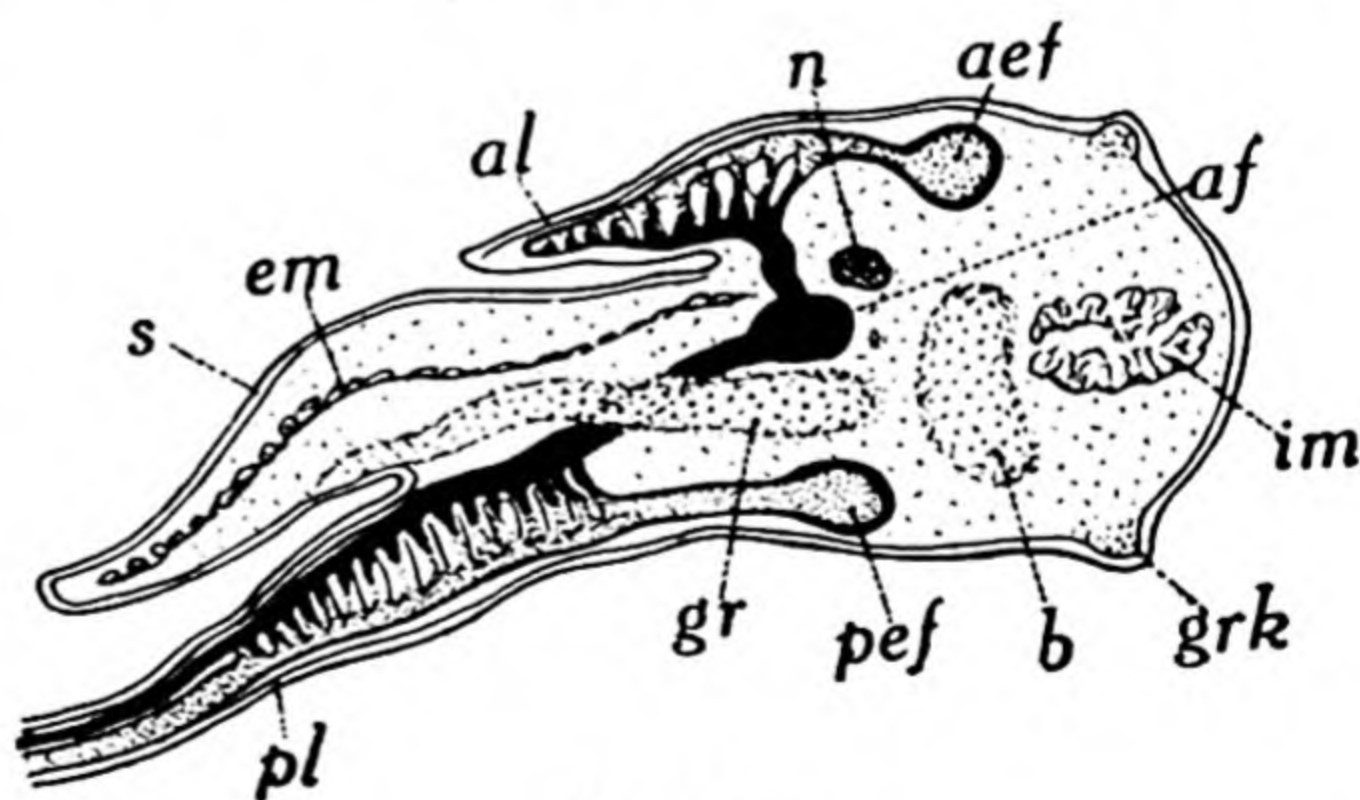

FIG. 516.

Section across gill-bar of *Scyllium canicula*, late embryo 32 mm. long, showing blood supply to lamellae. *aef* and *pef*, Anterior and posterior efferent vessels ; *af*, afferent vessel ; *al*, anterior lamella ; *b*, branchial bar ; *em*, external constrictor muscle ; *gr*, gill-ray ; *grk*, gill-raker ; *im*, adductor branchialis muscle ; *n*, nerve ; *pl*, posterior lamella continued into external filament, cut short ; *s*, gill-septum.

small transverse secondary folds (Riess, 799 ; Plehn, 797 ; Moroff, 793-4).
It is in these secondary folds that the respiratory exchange chiefly takes
place. They are thin plates the walls of which consist of a delicate flattened
outer ectodermal epithelium and a subepithelial layer of very thin under-
lying connective tissue ; covered by these epithelia is a middle vascular
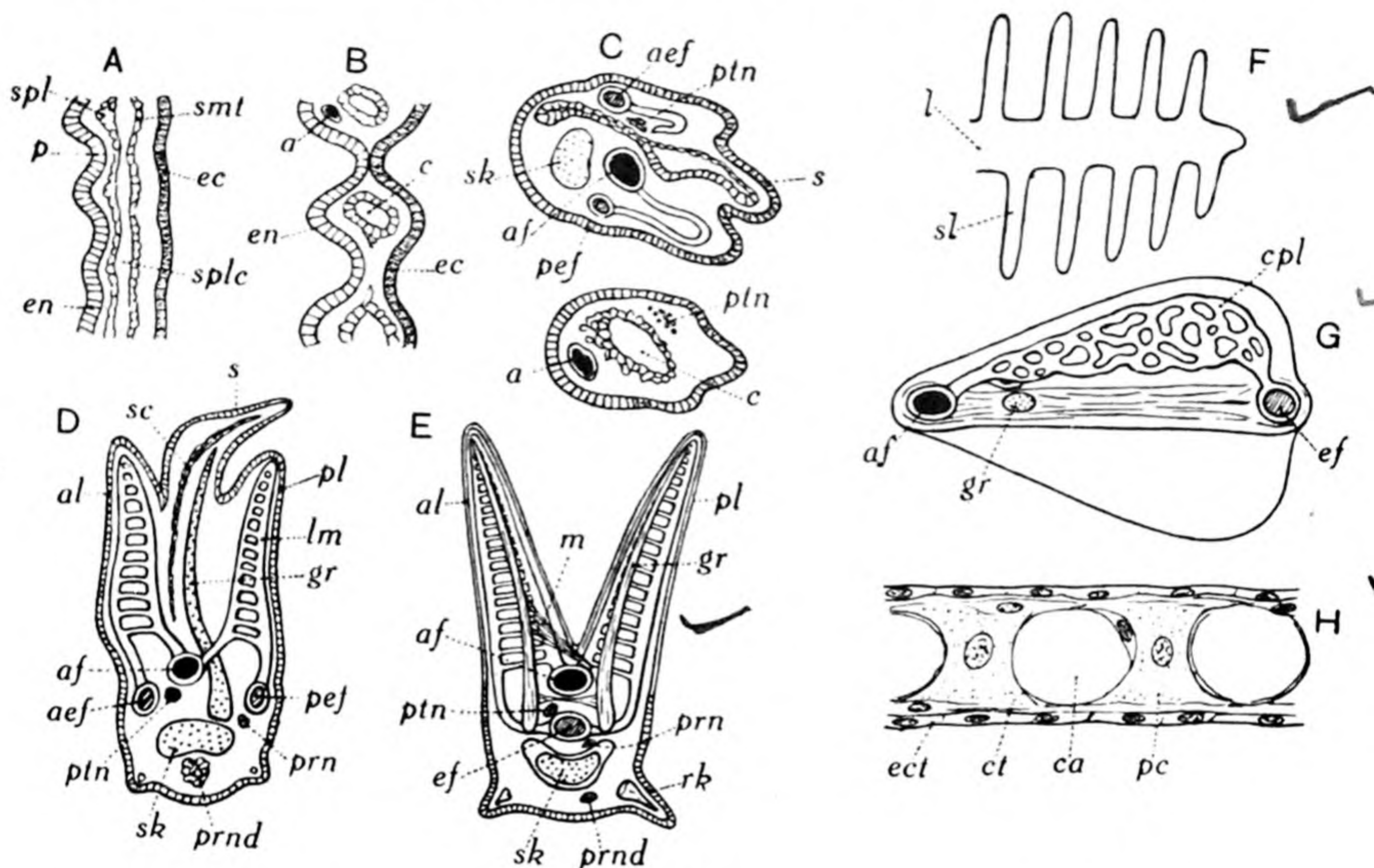layer with a network of capillaries through which blood flows from the

FIG. 517.

Diagrams illustrating structure and development of *gills* of a *Selachian*, A, B, C, D, and a *Teleostean*,
E, F, G, H.   A, Horizontal section of wall of pharynx at early stage when endodermal gill-pouches, *p*,
have not yet met ectoderm, *ec*, and splanchnocoele in lateral plate is still continuous, *splc* ; B, later
stage with lateral plate interrupted (cp. Fig. 514) ; C, still later stage (cp. Fig. 515) ; D and E, diagram-
matic transverse sections of gill-bars ; F, section along gill-lamella, *l*, to show disposition of secondary
lamellae, *sl*; G, section across gill-lamella showing circulation in secondary lamella ; H, section of
secondary lamella at right angles to surface.   *a*, Embryonic arterial arch ; *aef*, anterior efferent vessel
of arch ; *af*, afferent vessel of lamella ; *al*, anterior lamella ; *c*, coelom ; *ct*, cutis ; *ect*, ectoderm ;
ef, efferent vessel ; *en*, endoderm ; *gr*, gill-ray ; *lm*, capillary network ; *m*, lamellar muscle ; *pc*,
pilaster cells ; *pef*, posterior efferent vessel ; *pl*, posterior lamella ; *prn*, *ptn*, pre- and post-trematic
nerves ; *prnd*, branchial muscle ; *rk*, gill-raker ; *s*, outer region of septum ; *sk*, skeletal arch ; *smt*,
somatoblast ; *spl*, splanchnopleure.

afferent to the efferent limb of the vascular loop. Joining the opposite
walls and in the interstices of the network are peculiar pilaster cells first
described by Biétrix (775). This histological structure and the pilaster
cells occur not only in Pisces, but also in Cyclostomata, and even in
Amphibia (Faussek, 781), and may be taken as evidence that the gills are
homologous throughout the Craniata (p. 504).

The lamellae are disposed in close-set rows on the anterior and pos-
terior faces of a bar ; each row forms a hemibranch, while the front and
back row on a bar together make up a holobranch.

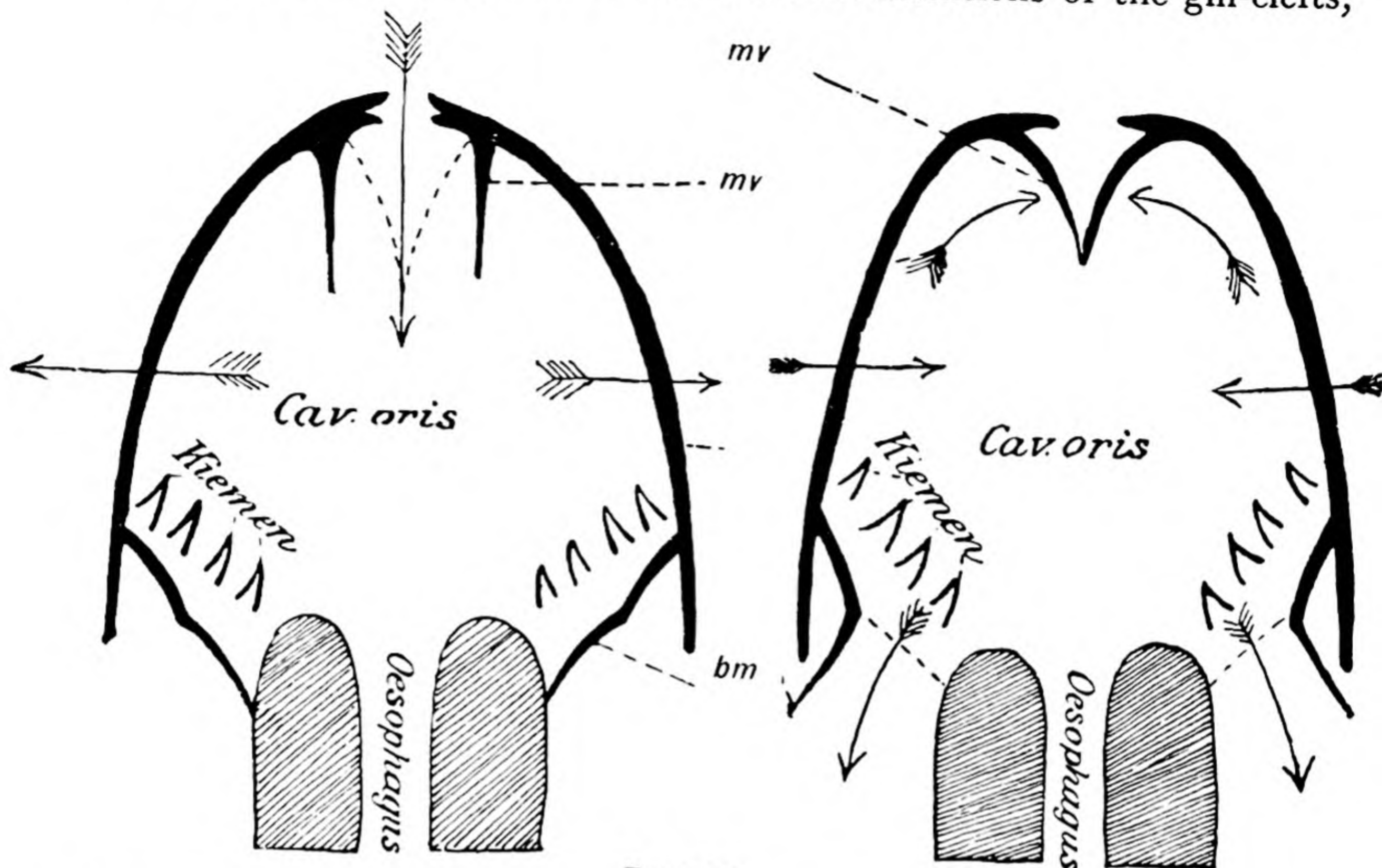We may now briefly review the chief modifications of the gill-clefts,

FIG. 517a.

Diagram illustrating the mechanism of respiration in Teleosts (after Dahlgren). A, Phase of inspiration; B, phase of expiration. In both figures the anterior oral part (*cav. oris*) represents a vertical section, and the posterior pharyngeal part enclosing the gills (*Kiemen*) a horizontal section. The arrows indicate the direction of the water-current and pressure, and those passing through the walls of the oral cavity the expansion and contraction of the opercular apparatus. In A, the maxillary and mandibular valves (*mv*) are open, and the branchiostegal membrane (*bm*) closed; in B, this condition is reversed.
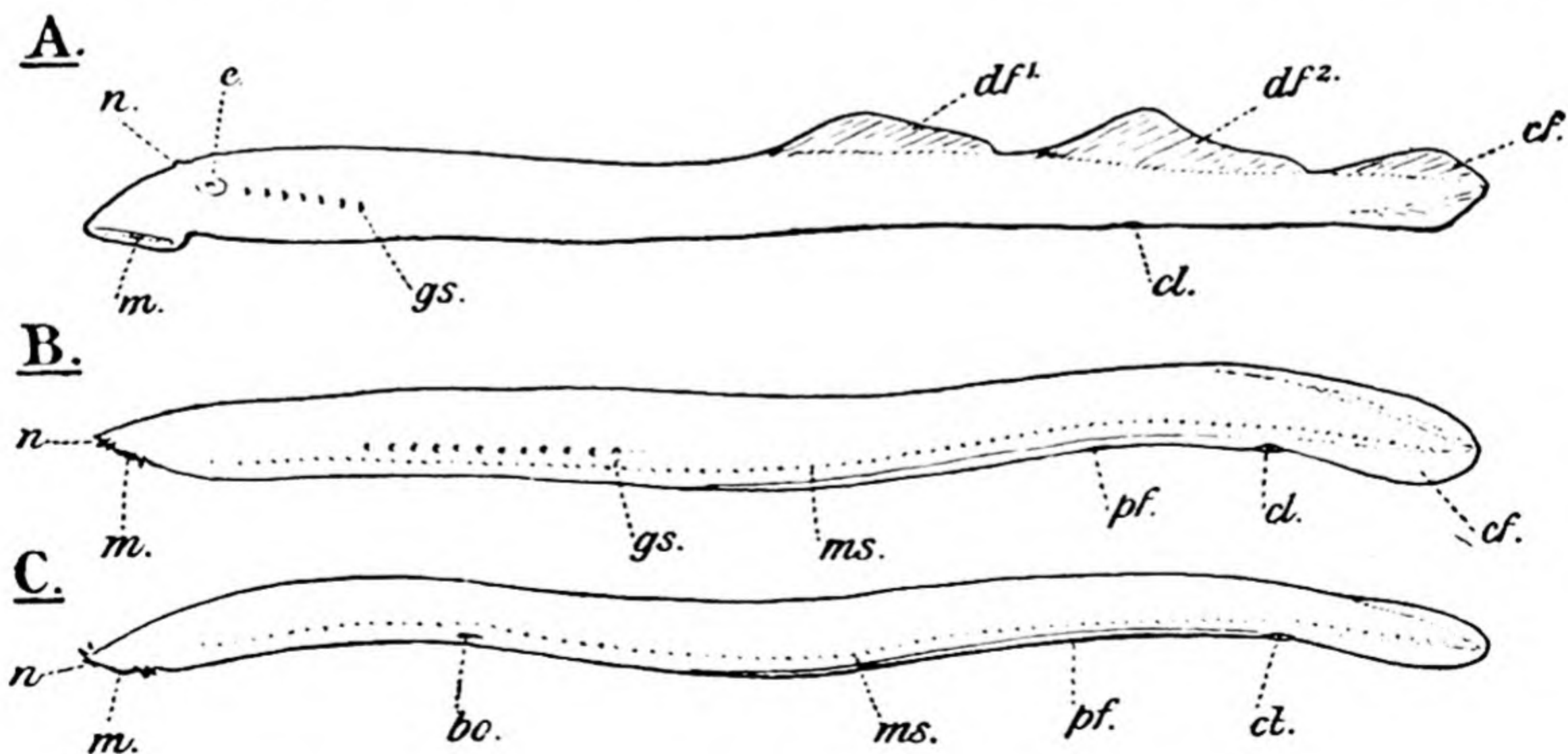
FIG. 518.

A, *Petromyzon fluviatilis*, L., the river Lamprey or Lampern. B, *Bdellostoma Dombeyi*, Lac. C, *Myxine glutinosa*, L., the Hag-fish. *bo*, Branchial opening; *cf*, caudal fin; *cl*, cloacal aperture; *df¹* and *df²*, first and second dorsal fin; *e*, eye; *gs*, gill-slit; *m*, mouth; *ms*, mucous sac; *n*, nostril; *pf*, preanal fin. (From Goodrich, *Vert. Craniata*, 1909.)

gill-bars, and gills in the various groups of Craniata (Oppel, **795**; Dohrn,

333). The gills of Cyclostomes are highly specialised structures, the branchial lamellae being enclosed in the adult in rounded sacs with narrow ducts leading into them from the alimentary canal, and out of them to the exterior; hence the name Marsipobranchii often applied to this group, Fig. 513. Their external openings are in the form of small rounded pores. Similar pores have been found in some Ostracodermi (Anaspida).

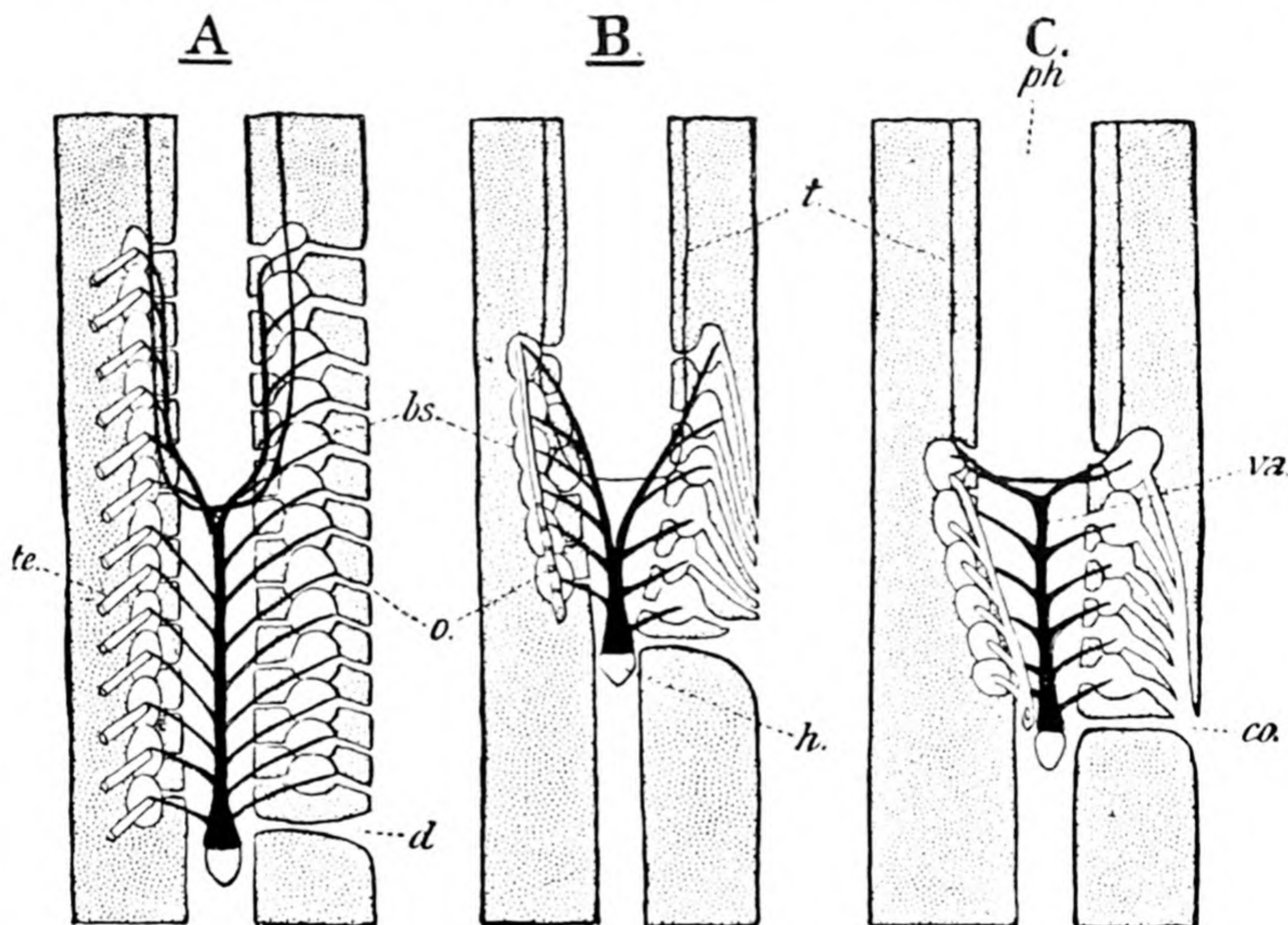Taking the Myxinoidea first (J. Müller, 1841; Dean, 155, 779),

FIG. 519.

Diagram of the gills and their afferent blood system in A, *Bdellostoma* (*Homea stouti*); B, *Paramyxine*; and C, *Myxine* (after Dean). Ventral view. *co*, Common opening of six gill-sacs and oesophageal duct; *bs*, gill-sac; *d*, oesophageal duct; *h*, heart; *o*, external opening of gill-sac; *ph*, pharynx; *t*, outline of rasping 'tongue'; *te*, tube leading to exterior; *va*, ventral aorta. (From Goodrich, *Vert. Craniata*, 1909.)

we find from 6 to 14 pairs of gill-sacs in the genus *Bdellostoma*, and 6 (sometimes 7) in *Myxine*. But while in the more primitive *Bdellostoma* the external ducts open separately, in *Myxine* they combine to a single opening posteriorly. An interesting intermediate condition has been described by Dean in *Paramyxine*, where the pores are closely approximated. The condition in *Myxine* is obviously secondary, Figs. 518-19.

In addition to these gill-sacs there is in all Myxinoids a 'pharyngocutaneous duct' passing on the left side from the pharynx to the exterior behind the last sac; its opening is adjacent or confluent with the last

left gill-pore, Figs. 519-20. It is conjectured that this gill-less duct has been derived from a visceral cleft. Breathing takes place by the expansion and contraction of the muscular walls of the sacs; water being drawn in through the median 'nostril', Fig. 518, which leads into a hypophysial canal opening into the pharynx behind, and expelled to the exterior along the expiratory tubes. When the Myxinoid is feeding and its head is buried in its prey, water may still pass in and out by these tubes. It is no doubt to facilitate this respiration that the gill-sacs in Myxinoids are situated very far back and the expiratory tubes lengthened so as to carry the external openings still farther from the head. This quite exceptional disposition of the gills is secondary. The visceral clefts develop in the usual position; but, excepting for the first pair which remain stationary and later disappear, they shift backwards (together with the heart, etc.) at a later stage (Dean, 778).

The Petromyzontia preserve the primitive separate external pores, but in the adult the sacs open internally into a median branchial tube situated below the oesophagus. This branchial tube is blind behind and opens in front into the pharynx just behind the valve derived from the larval velum. In respiration water may enter the mouth; but when this is not possible, owing to the oral sucker being fixed or closed, water is pumped in and out of the contractile sacs through the expiratory tubes. The Ammocoete larval

FIG. 520.

Skeleton of the anterior region of *Bdellostoma Dombeyi*, Lac. (After Ayers and Jackson.) *ac*, Auditory capsule; *bpl*, basal plate of rasping organ; *br*¹⁻³, first three branchial arches; *brc*, branchial cartilage; *bro*, branchial opening; *cc*, cornual; *cr*, nasal ring; *dp*, dental plate; *dt*, dorsal 'tongue' cartilage; *hp*, hypophysial plate; *lb*, labial; *mpl*, middle plate; *nac*, nasal capsule; *nc*, notochord; *ntb*, neural tube; *od*, opening of last gill-pouch and of oesophageal duct; *oe*, oesophagus; *pq*, suborbital arch; *to*, 'tongue' cartilage; *top*, posterior ventral 'tongue' cartilage; *tr*, trabecular arch; *vb*, velar skeleton; 1-4, cirrhi. (From Goodrich, *Vert. Craniata*, 1909.)

stage possesses gill-pouches which open in the usual manner by wide slits into the pharynx, and it is at metamorphosis that the blind
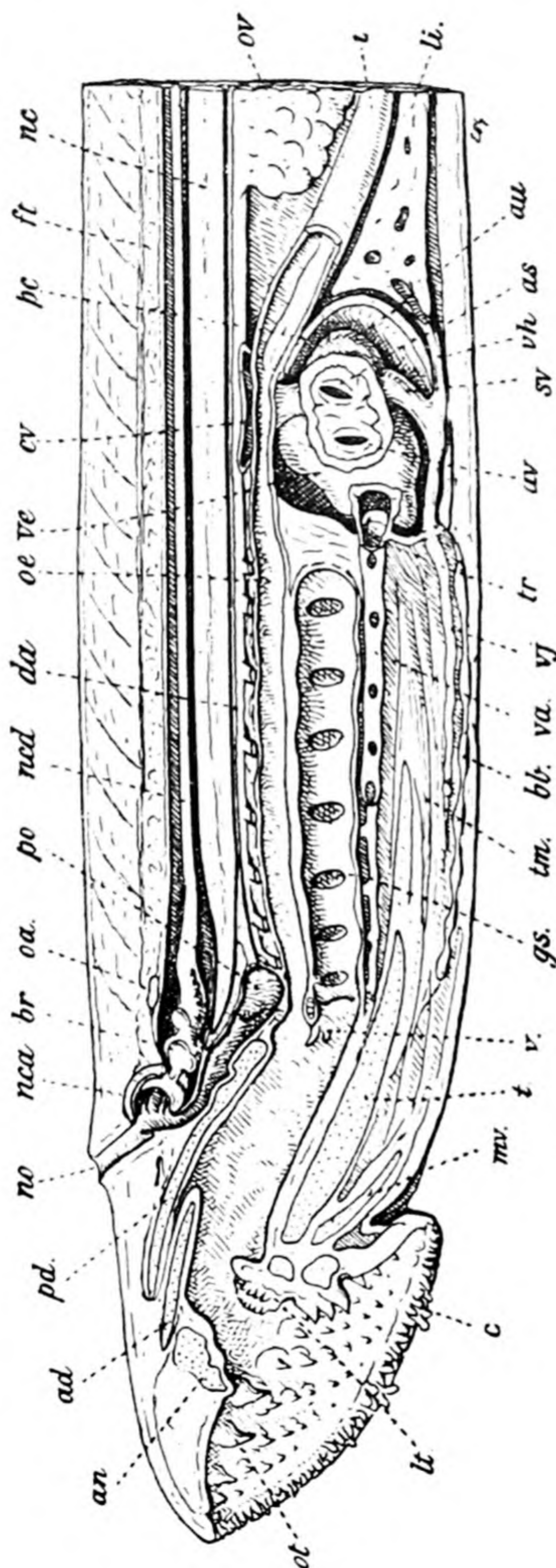

FIG. 521.

Longitudinal section of the anterior region of *Petromyzon marinus*, L. *ad*, Anterior dorsal cartilage; *an*, annular; *as*, sinu-atrial opening and valves; *au*, atrium opened up; *av*, atrioventricular opening and valves; *bb*, branchial basket; *br*, brain; *c*, marginal cirrhi; *cv*, entrance of cardinal veins into sinus venosus; *da*, dorsal aorta; *ft*, fatty tissue; *gs*, gill-slit; *i*, intestine opened to show spiral valve; *li*, liver; *lt*, teeth on rasping 'tongue'; *mv*, median ventral cartilage; *nc*, notochord; *nca*, nasal capsule; *ncd*, spinal cord; *no*, median nostril; *oa*, occipital arch; *oe*, oesophagus; *ot*, horny tooth; *ov*, ovary; *pc*, pericardium; *pd*, posterior dorsal cartilage; *po*, hypophysial sac; *sv*, sinus venosus; *t*, 'tongue' cartilage; *tm*, 'tongue' muscle; *tr*, bulbus arteriosus opened to show valve; *v*, velar tentacles; *va*, ventral aorta, median behind the 4th afferent gill-artery; *ve*, ventricle; *vh*, ventral hepatic vein; *vj*, ventral jugular vein. The cartilages are dotted. (From Goodrich, *Vert. Craniata*, 1909.)

respiratory tube becomes separated off below from the oesophagus which extends forwards above, Figs. 521-3.

The gill-lamellae of Cyclostomes resemble those of Pisces in having transverse secondary vascular folds across them on both sides, and are

set in an almost complete ring inside the sacs of the adult, interrupted, however, dorsally and ventrally by a fold. In the Ammocoete they are normally disposed as hemibranchs, one on each side of each gill-
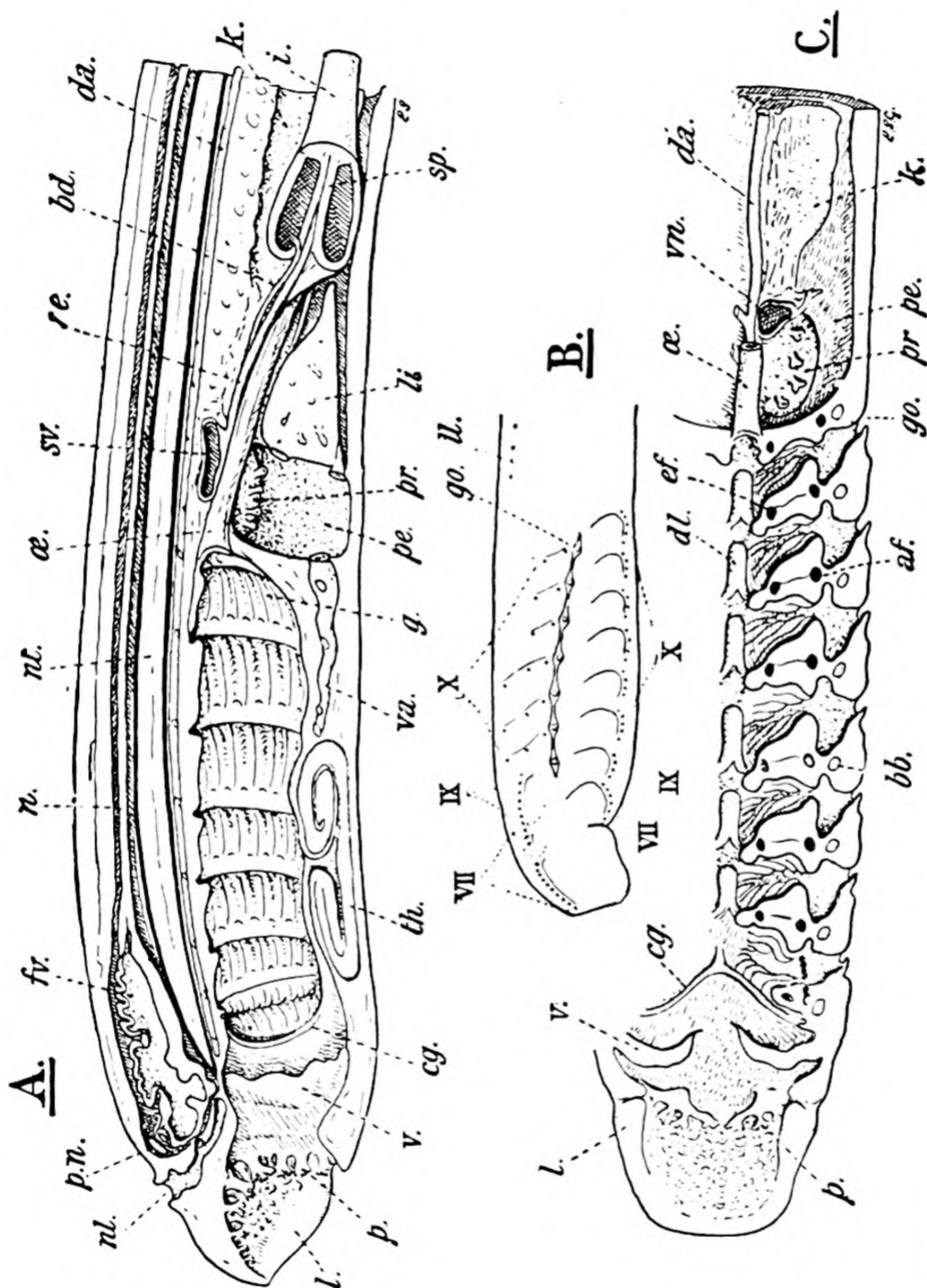

FIG. 522.

Ammocoete larva of *Petromyzon fluviatilis*, L. A, Enlarged sagittal section; B, left-side view of anterior region (after Alcock); C, horizontal longitudinal section passing through the gills, etc., represented on the right side only, seen from below. *af*, Afferent branchial vessel; *bb*, branchial basket; *bd*, bile-duct; *cg*, ciliated groove; *da*, dorsal aorta; *dl*, lobe of dorsal lamina; *ef*, efferent branchial vessel; *fv*, cavity of brain; *g*, gill; *go*, gill-opening; *i*, intestine; *l*, lip; *li*, liver; *ll*, trunk lateral-line organs; *k*, kidney (mesonephros); *n*, nerve-chord; *nl*, median nostril; *nl*, notochord; *oe*, oesophagus; *p*, papilla; *pe*, pericardium from which the heart has been removed; *pn*, pineal eye; *pr*, pronephros; *sp*, spiral valve exposed in intestine; *sv*, entrance to sinus venosus; *th*, thyroid gland; *v*, velum; *va*, ventral aorta; *ve*, intestinal vein; *vn*, sinus venosus; VII, IX, and X denote lateral-line organs supplied from the facial, glossopharyngeal, and vagus nerves. (From Goodrich, *Vert. Craniata*, 1909.)

pouch. The gill-bars, however, differ from those of Pisces : they project deeply into the cavity of the pharynx, and become differentiated into outer and inner regions ; the skeletal arch being in the outer region close to the skin, and the respiratory lamellae and blood-vessels being borne by the inner region, Figs. 522-3-4 (see p. 504). This exceptional and

characteristic relative position of arch and gill is preserved in the adult,
where the arches combine in Petromyzontia to form a delicate ' branchial
basket ', and in Myxinoids remain as vestigial cartilages near the external
gill-openings (separate in *Bdellostoma*, and combined to a complex car-
tilage in *Myxine*), Fig. 520.

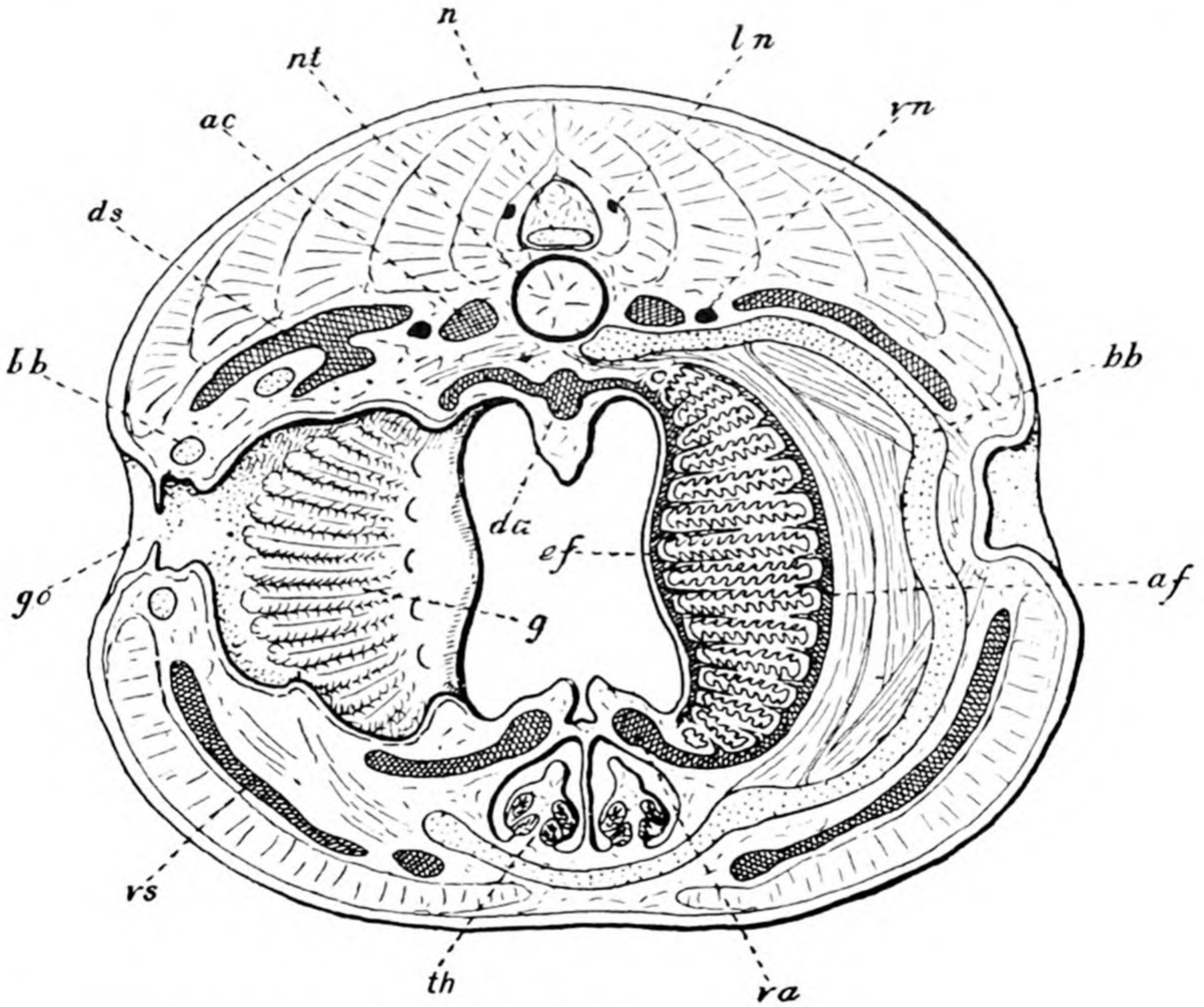In Pisces both the internal and external gill-openings are dorso-

FIG. 523.

Transverse section of the gill region of an Ammocoete larva, somewhat diagrammatic. (Partly
after Alcock.)   *ac*, Anterior cardinal vein ;   *af*, afferent artery ;   *bb*, branchial basket ;   *da*, dorsal
aorta ;   *ds*, dorsal blood-sinus ;   *ef*, efferent artery ;   *g*, gill-lamella ;   *go*, gill-opening ;   *ln*, lateral-
line nerve ;   *n*, nerve-cord ;   *nt*, notochord ;   *th*, thyroid gland ;   *va*, ventral aorta ;   *vn*, vagus nerve ;
vs, ventral blood-sinus.   (From Goodrich, *Vert. Craniata*, 1909.)

ventrally elongated and narrow, the pouches being compressed. In
Selachii a hemibranch of gill-lamellae occurs on the anterior and posterior
side of each branchial arch except the last, which is gill-less, Figs. 513,
532. A posterior hemibranch is also present on the hyoid arch (and on
the mandibular arch, see below, p. 519). Water is taken in at the mouth
and expelled through the slits ; but in bottom-living forms like the Raji-
formes, where the branchial slits are ventral, it may enter through the
enlarged spiracle provided with a movable valve (p. 519). The gill-bar is

differentiated into an inner region containing the skeletal visceral arch, and a thin outer region containing the blood-vessels, etc., and bearing the gill-lamellae ; this gill-septum being complete passes beyond the lamellae into the outer denticle-bearing skin surrounding the opening, and is supported by a single posterior row of cartilaginous gill-rays (p. 398). In the young stages the external openings are elongated dorso-ventrally, but in the adult they often become relatively shortened.
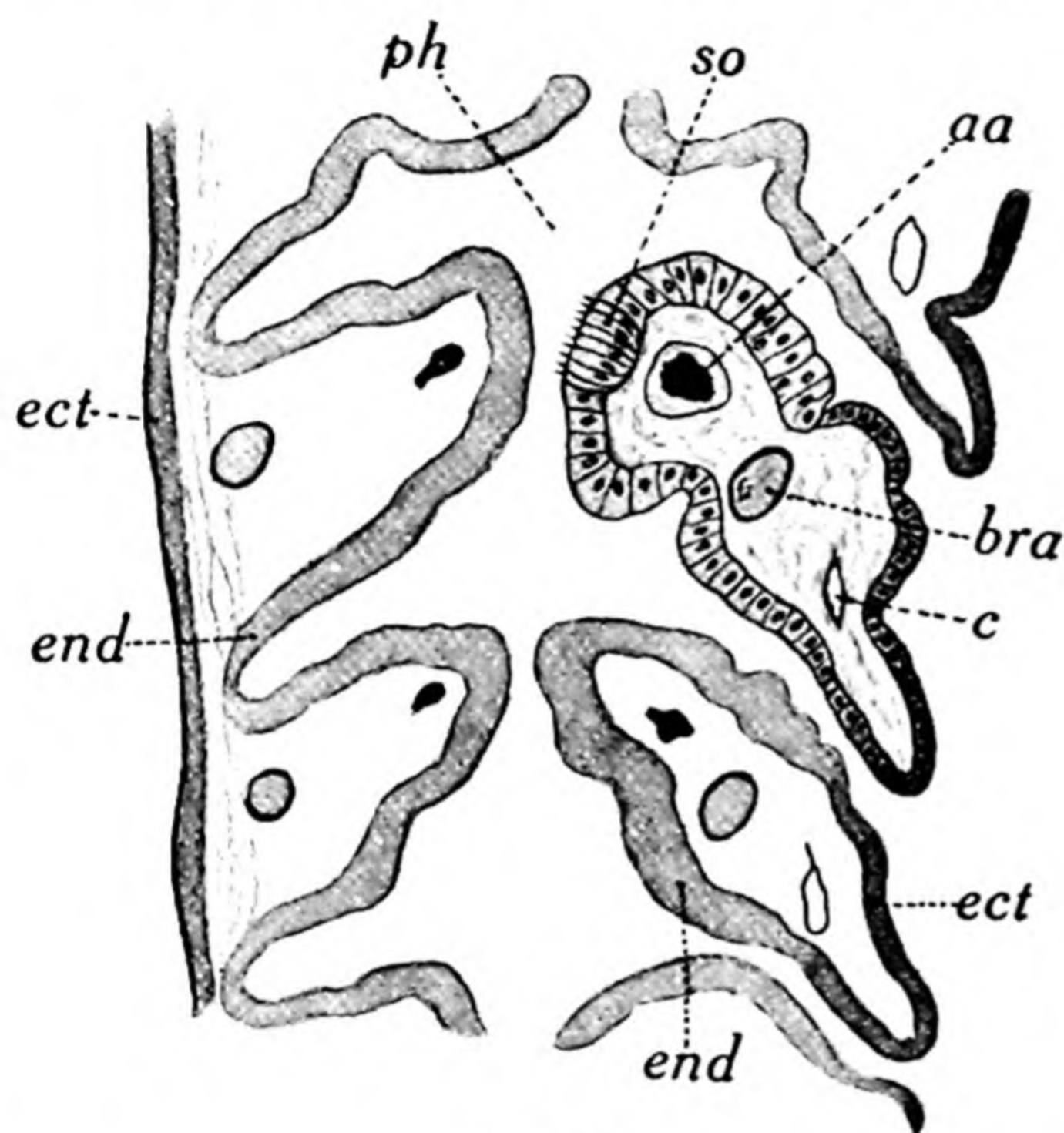

FIG. 524.

Petromyzon, young ammocoete larva ; slightly oblique horizontal section through pharynx and gill-slits, passing through openings on right and above them on left. *aa*, Arterial arch ; *bra*, skeletal arch ; *c*, coelomic canal ; *ect*, ectoderm ; *end*, endoderm ; *ph*, lumen of pharynx ; *so*, sense organ.

The more primitive forms, however, preserve wider openings over which the edge of the septum extends as a backwardly directed valvular flap particularly well-developed in *Chlamydoselachus*, Fig. 27.

The enlargement of this flap on the hyoid bar leads to the condition seen in Holocephali, where it forms a large operculum covering all the branchial slits. The gills of these specialised Elasmobranchs are built on the same plan as those of Selachii (there are a posterior hyoidean hemibranch, holobranchs on the first three branchial bars, and an anterior hemi-branch on the fourth), but consequent on the development of the operculum the outer portions of the gill-septa are reduced. Cartilaginous gill-rays remain in the opercular flap, but are lost on the branchial bars, Figs. 428, 444. This operculum has, no doubt, been developed independently of that characteristic of the Osteichthyes. The provisional embryonic and larval external gills of Elasmobranchs and other forms will be dealt with later (p. 501).

All the Osteichthyes are primitively provided from the hyoid bar with a large opercular fold strengthened by opercular bones and covering all succeeding branchial slits, which open into a subopercular branchial chamber. Water is taken in at the mouth, passed through the slits, and expelled from the chamber into which project the gill-lamellae, through an opening now bounded behind by the dermal pectoral girdle. Appro-

priate movements of the branchial bars and operculum, helped by breathing valves or folds developed in many of the higher Teleostomes on the inner margin of the upper and lower jaws, propel the respiratory current backwards, Fig. 517a. This current may be strong and used in locomotion.
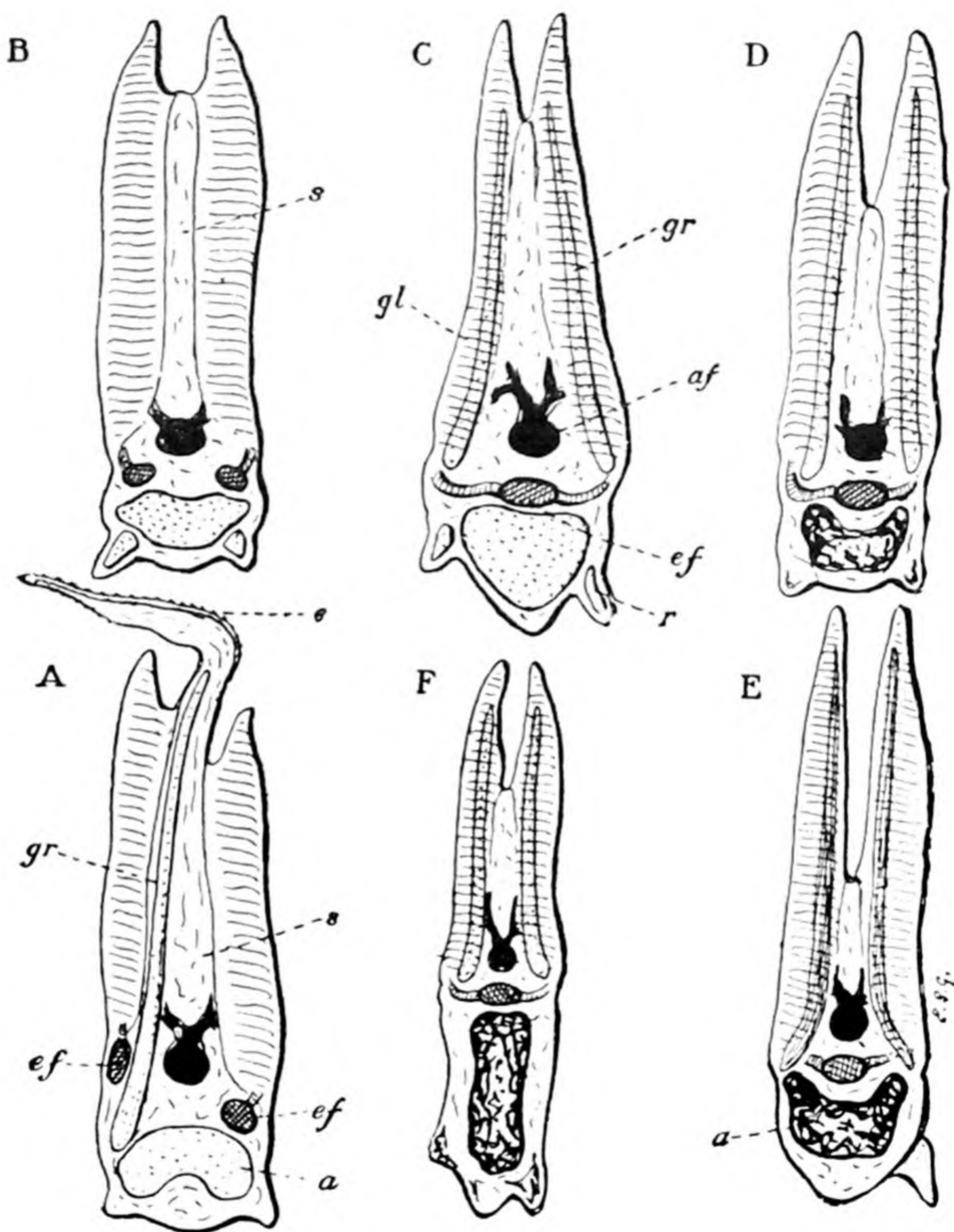

FIG. 525.

Sections across the gill-arch of A, *Mustelus*; B, *Ceratodus*; C, *Acipenser*; D, *Lepidosteus*; E, *Salmo*; F, *Polypterus*. *a*, Skeletal arch; *af*, afferent artery (black); *e*, septum reaching external surface; *ef*, efferent artery (cross hatched); *gl*, gill-lamellae; *gr*, supporting gill-ray; *r*, gill-raker; *s*, septum, largest in A, and smallest in E. Anterior lamellae to the right. (From Goodrich, *Vert. Craniata*, 1909.)

The septa on the branchial bars are reduced and never project beyond the lamellae, Fig. 525. Probably also on account of the great development of the operculum the hyoidean posterior hemibranch is retained only in *Ceratodus*, Chondrostei, and *Lepidosteus*. A mandibular pseudo-branch is usually present (p. 519).

Among living Dipnoi the respiratory function of the gills seems to be

on the decline and is supplemented by that of the lung-sacs (so-called air-bladder, p. 594), an adaptation to life in rivers apt to become dried up or foul in certain seasons of the year. *Ceratodus* retains the most primitive gills (four holobranchs on the first four branchial bars and a hyoidean pseudobranch), Figs. 534, 535; in *Lepidosiren* the hyobranchial or first branchial slit is closed and there are only three holobranchs. *Protopterus*, in which the gills are much reduced, has none at all on the first and second branchial bars, a holobranch on the third and fourth, and on the fifth bar an anterior hemibranch which is possibly merely an extension of the one in front. The hyoidean hemibranch is here a true gill. No gill-rays are present, and the lamellae extend beyond the septum.

In the Teleostomi the branchial bars become slender, and the slits between them narrow and much elongated; the septum is progressively reduced, while the pointed lamellae project freely into the branchial chamber. Two rows of gill-rays occur on each arch, extending not into the septum but into the respiratory lamellae, Figs. 517, 525. Similar rays may occur in the pseudobranch (p. 520).

Polypterus has no hyoidean hemibranch, and the fourth branchial arch has an anterior hemibranch only, there being no slit or skeletal arch behind it.

The Chondrostei are provided with five branchial slits, four holobranchs, and a hyoidean hemibranch. Five slits and four holobranchs on the branchial bars are found in Amioidei, Lepidosteoidei, and Teleostei (with few exceptions in specialised forms). *Lepidosteus* alone among Holostei preserves the hyoidean hemibranch (see below, p. 517).

The primitive Tetrapoda no doubt inherited true gills from their fish-like ancestors, which gills served for respiration at all events in the aquatic larval stage during the transition to terrestrial life. It is probable that they also inherited an operculum, though no trace of opercular bones has yet been found in any fossil or living Tetrapod. Traces of four branchial arches have been described in the young of several Stego-cephalia. That they were similar to the gill-bearing arches of fish, and were even retained as such in some of the adult Branchiosauridae, is evidenced by the disposition of the fossilised gill-rakers (Credner, 484; Fritsch, 23; Bulman and Whittard, 465a). Among modern Tetrapods internal gills occur only in the tadpole larvae of Anura in the form of two rows of branching filaments on the bars separating four open gill-slits, Fig. 541; hyoidean membranous opercular folds cover over the gill region and even the developing pectoral limbs. Paired branchial openings are formed in Aglossa, but in most other Anura where the two chambers communicate

below only one opening remains on the left side until the fore-limbs emerge. In the young of other modern Amphibia there are no internal gills and no opercular folds of any size, and the extensive operculum of Anura is probably to a great extent a new formation.

The four branchial slits pierced in Anura and Apoda are closed in the adult where respiration is pulmonary and cutaneous (p. 547) ; but among the Urodela which are readapted to an aquatic adult life some of them may remain open (third in *Menopoma* and *Amphiuma* ; second and third in Proteidae ; first, second, and third in Sirenidae).

The Amniota have lost all trace of gills as respiratory organs, and the slits themselves open for but a short time in Reptiles and Birds, and not
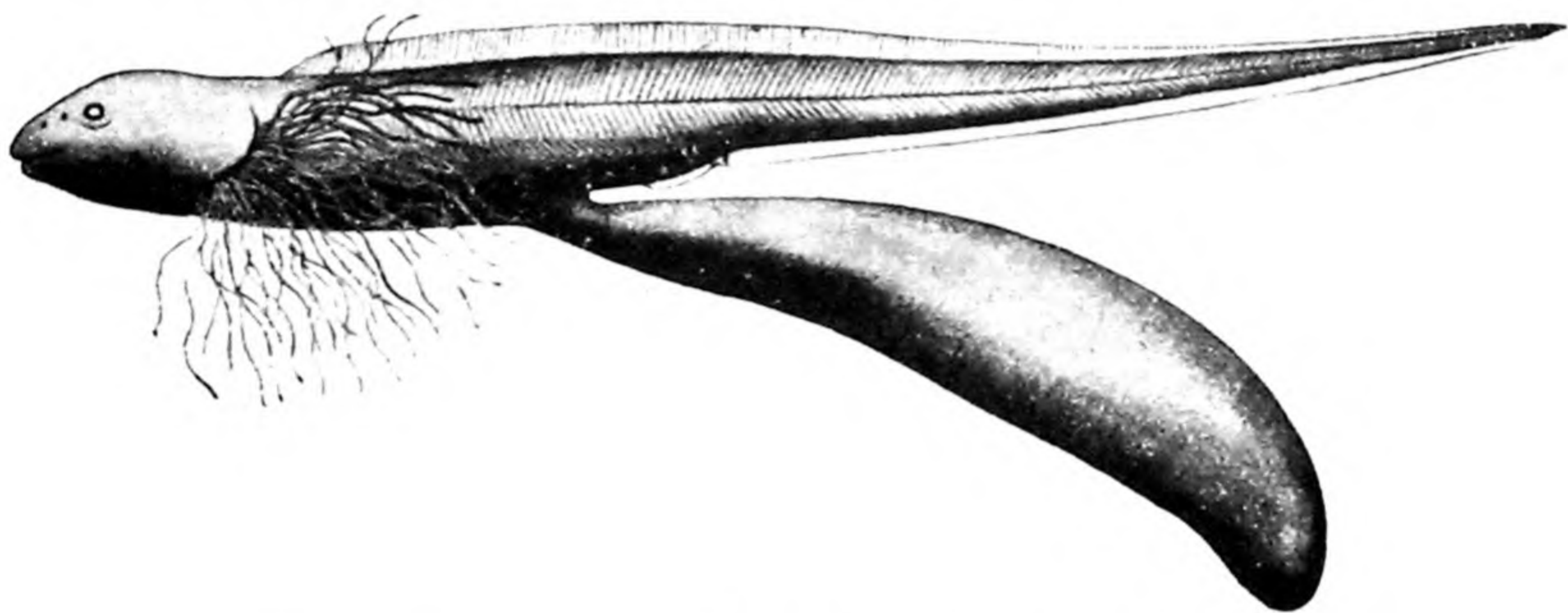
FIG. 526.

Larva of *Gymnarchus niloticus* ; tenth day (from Kerr, *Embryology*, 1919).

at all in most Mammals. The embryonic vestigial slits may be marked externally by grooves, lodged in a deep lateral depression called the cervical sinus, which later is overgrown and closed by the hyoid arch and a fold from above and behind.

External Gills.—In addition to the true or internal gills there may be developed provisional superficial gills. These external gills are of two kinds, which may be distinguished as true external gills and external gill-filaments, Figs. 146, 515-16, 526. The latter occur in the early stages of all Elasmobranchs, and are long filamentous prolongations of the outer tips of the young internal gill-lamellae of all the posterior hemibranchs. Each filament is supplied with a vascular loop passing from the afferent to the efferent branchial vessel, and floats in the albuminous fluid within the egg-case. These filaments probably serve not only for respiration, but also for the absorption of food-material. They disappear when the fish hatches. Similar external gill-filaments have been found in certain larval Teleostomes (Chondrostei, some Teleostei, and especially Mormyridae : Budgett, **776** ; Assheton, **774**).

True external gills occur in the embryonic or free larval stages of Dipnoi (except *Ceratodus*), of Polypterini, and of Amphibia, Figs. 527-8, 541-2. They usually develop early, even before the slits are pierced and before the opercular fold is formed, as outgrowths from the dorsal outer surface of one or more of the gill-bars. They contain vascular loops derived from the aortic arches, and are covered by ectodermal epithelium sometimes ciliated. Usually they are provided with muscles, are movable and retractile. Four pairs of pinnate external gills are developed on the four branchial bars of *Protopterus* and *Lepidosiren* (Budgett, 776; Kerr, 790). When the operculum develops they become crowded together above
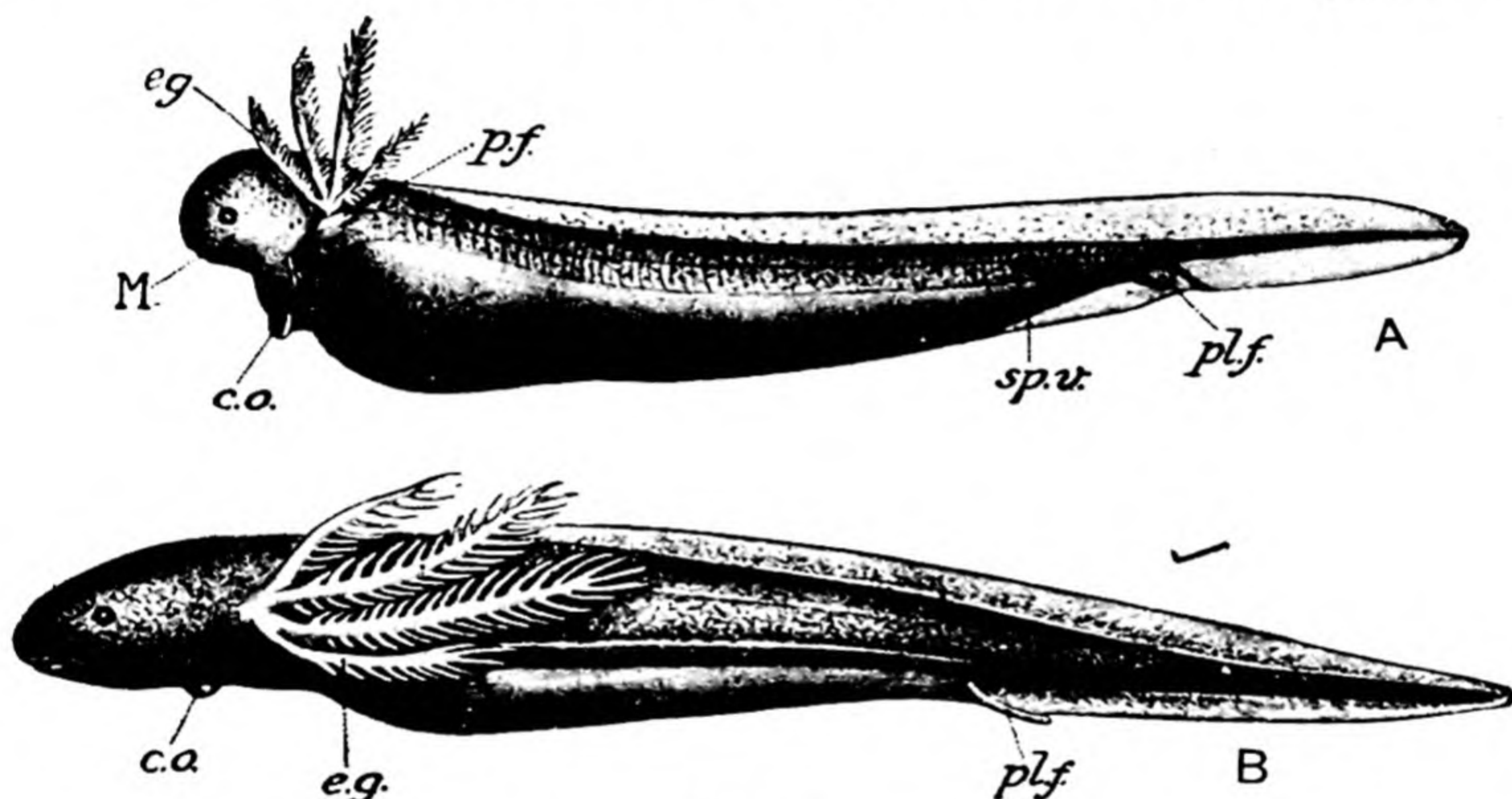
FIG. 527.

Stages in the development of *Lepidosiren paradoxa*. A, Stage 33; B, 35. *c.o*, Cement organ; *e.g*, external gill; *M*, mouth; *p.f*, pectoral fin; *pl.f*, pelvic fin; *sp.v*, spiral valve of intestine. (From Kerr, *Embryology*, 1919.)

its posterior border. *Protopterus* is remarkable in that it usually retains the three posterior external gills in a reduced condition even in the adult, Fig. 535. The larva of *Polypterus* has only one pair of external gills (Steindachner, 1869; Budgett, 10, 776; Kerr, 791). They are large, pinnate, with a strong axis supported by a short cartilaginous ray, and are developed from the hyoid bar (Kerr). The external gills of Amphibia are usually purely larval organs (Anura and Apoda), but the Urodela being more or less readapted to an aquatic life tend to retain them in the adult as important organs of respiration. In the Perennibranchiata, then, they develop into permanent large arborescent gills on the first three branchial bars (Clemens, 777; Boas, 813; Maurer, 849).[1]

[1] A pair of slender processes, known as 'balancers', occur on the head of the larva of many Urodela (Amblystomidae, Salamandridae, and Hynobiidae), and were first described by Rusconi, 1821. They have been thought

The origin and morphological significance of the true external gills are still somewhat obscure. For Kerr's suggestion that they are ancient organs which preceded and perhaps even gave rise to the internal gills
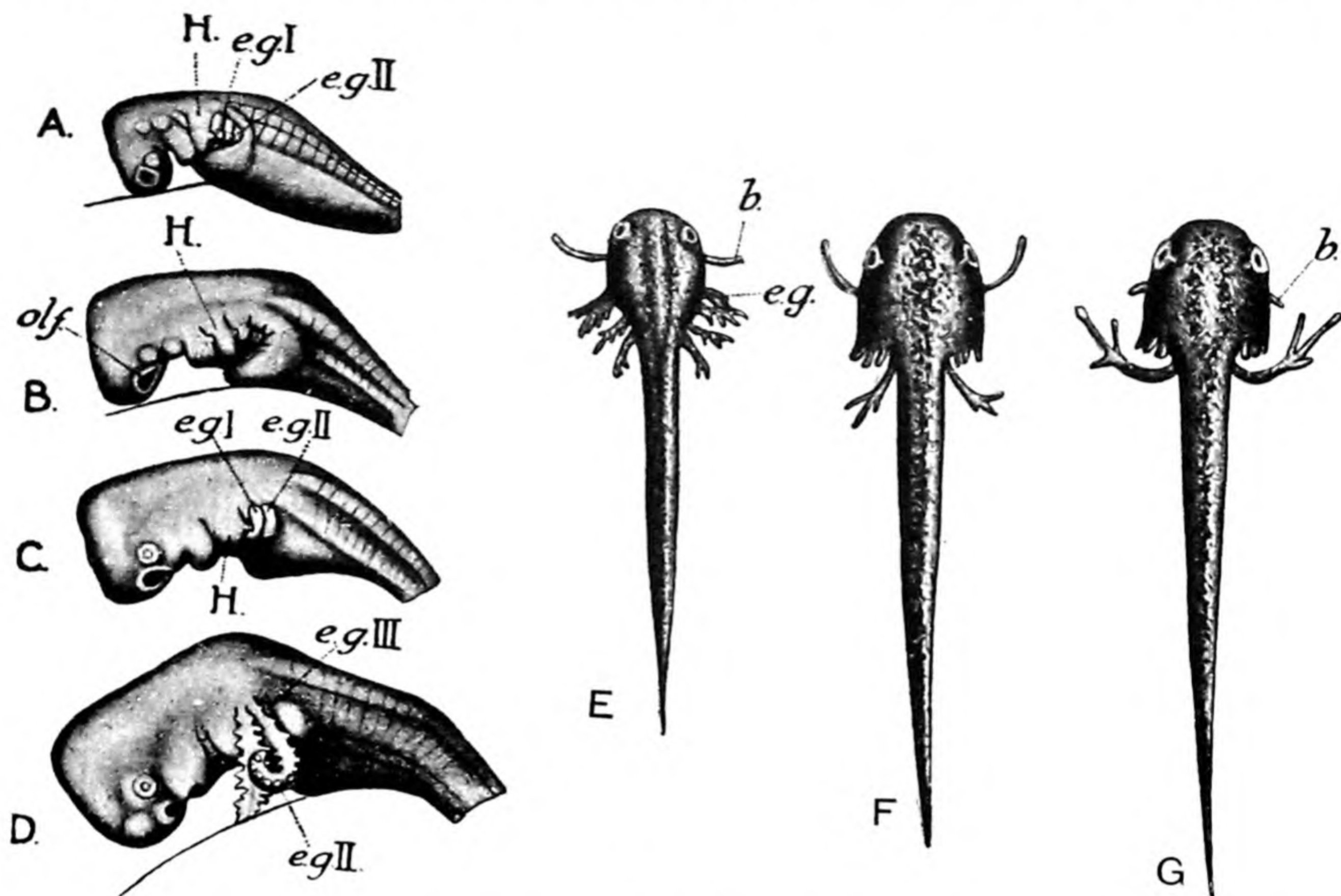

FIG. 528.

A-D, *Hypogeophis* embryos showing development of the external gills. (After Brauer, 1899.) *e.g*, External gill ; *H*, hyoid arch ; *olf*, olfactory organ. The rounded knobs seen projecting in B from the hyoid arch, and also from the mandibular arch in front of it, are possibly external gill rudiments which do not go on with their development. E-G, Three stages in larval development of a newt (*Triton taeniatus*) as seen from above. (After Egert, 1913.) *b*, Balancer; *e.g*, external gill of first branchial arch. In Fig. A what looks like a posterior external gill is the pectoral limb. In Figs. B and C the external gills have been cut away leaving only their basal stumps. (From Kerr, *Embryology*, 1919.)

there seems to be little evidence, since they are found neither in Cyclostomes nor in Elasmobranchs. Nevertheless, they possibly were present as larval organs in the common ancestor of the Osteichthyes and

by some to represent hyoidean external gills, but for this view there is no good evidence. The balancers have recently been studied in detail by Harrison (785). They are supporting and adhesive processes, are covered at their tips by glandular epithelium and strengthened by a thick basement membrane ; a nerve runs up them and they contain no muscles. The blood-supply is derived from a branch of the hyoidean artery, but is returned not to the aorta but to the jugular vein (Maurer, 849). The balancers are probably homologous with the adhesive organs of larval Anura. They develop early on the mandibular arch, are indeed borne on a knob of the palatoquadrate cartilage, and drop off when the pectoral limbs are sufficiently developed to support the head, Fig. 528.

Tetrapoda, and Bulman and Whittard have recently described three pairs of external gills in *Branchiosaurus* from the Permian (465a), a Stegocephalian apparently readapted to an aquatic life like the modern Urodele.

FIG. 529.

A, B, Horizontal sections through salmon embryos explaining position of pseudobranch on inner surface of operculum. (After Goette, 1901.) *A.r*, aortic root; *aa*, aortic arch; *an*, anastomotic vessel connecting aortic arches I and II; *Hy*, hyoid arch; *op*, operculum; *Ph*, cavity of pharynx; *ps*, pseudobranch; *vc*, visceral cleft. C, Horizontal section through branchial region of young *Acipenser* showing the ectodermal origin of the gill-lamellae. (After Goette, 1901.) *aa*, Aortic arch; *g.l*, rudiment of gill-lamella; *Hy*, hyoid arch; *op*, operculum; *Ph*, cavity of pharynx (From Kerr, *Embryology*, 1919.)

Following Boas (812-13) and Gegenbaur (170) we may consider the external gills as specialised dorsal gill-lamellae, belonging originally to the so-called internal gills, which have grown outwards together probably with a portion of the gill-septum forming the axis. These external gills would, then, be specialised regions of the gills enlarged and precociously developed for larval respiration.

Two further questions remain to be discussed concerning the gill-lamellae. Are they products of the ectoderm or of the endoderm, and are they homologous throughout the Craniata?

Goette (782, 783), having studied their development in various groups, concluded that they are of endodermal origin in Cyclostomes, but that they are of ectodermal origin in all other Pisces and in Amphibia, with the exception of the spiracular gill, which he believed to be endodermal. These conclusions have not been generally accepted and have given rise to much controversy. That Goette was mistaken in attributing a different origin to branchial and spiracular lamellae there can be little doubt; but whether in the Elasmobranchii they are covered by ectoderm or endoderm it is difficult to determine, since before they appear the slits have been pierced and the limit between the two germ-layers has already vanished.

Dohrn, while maintaining that the most important constituent of the gill is the blood-vessel, held that the lamellae are chiefly covered with ectoderm. Certainly in Teleostomes, where the lamellae sprout outwards before the membranes closing the slits have been broken through, as Goette showed in *Acipenser*, there can be no doubt that they are covered
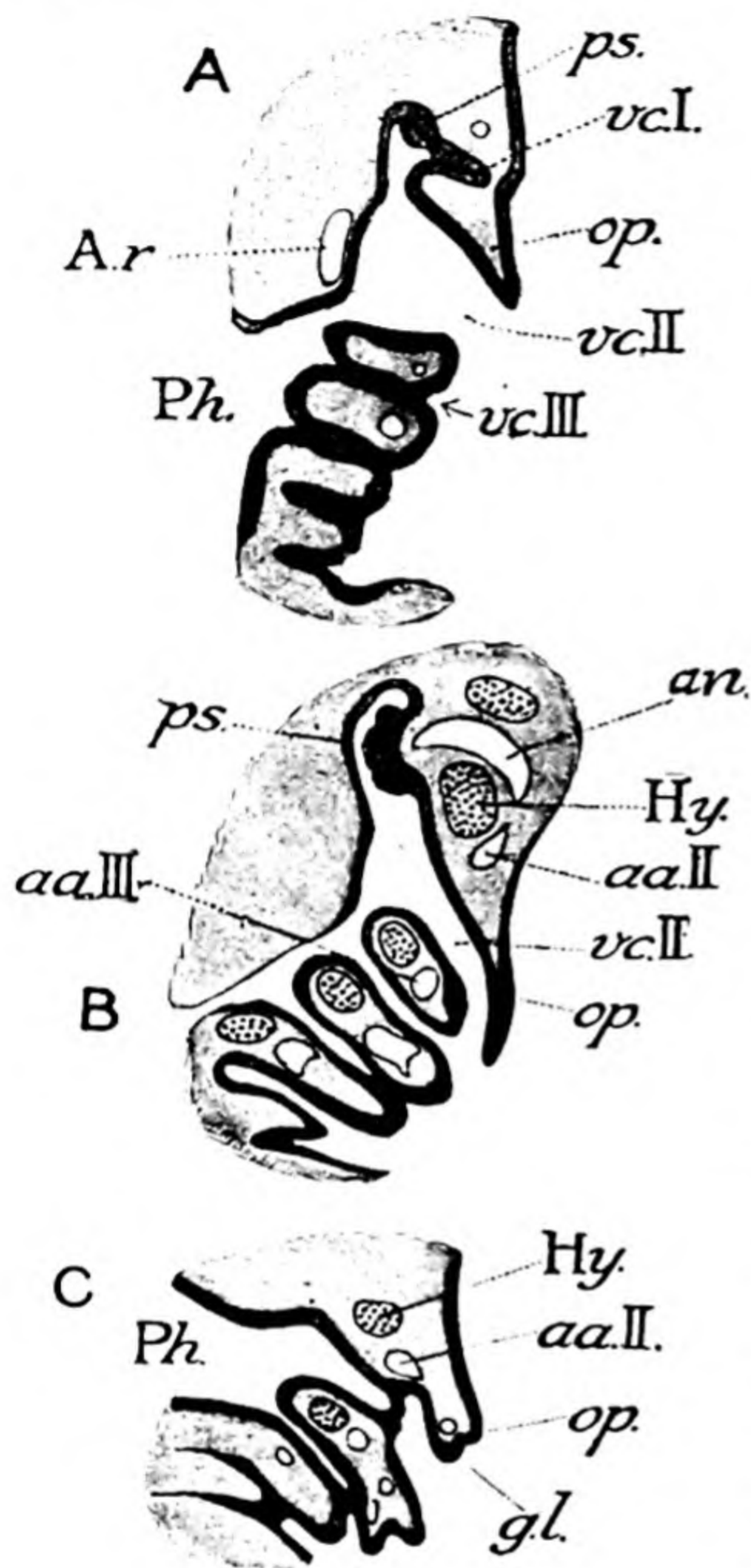
by ectoderm, Figs. 528-9. Kellicott (789) describes the ectoderm as growing inwards and covering the lamellae in *Ceratodus*. Even more obviously does ectoderm cover the external gills of Pisces and Amphibia. Greil, however, attempted to prove that both layers covered the gill-lamellae of Dipnoi and Amphibia, endodermal cells extending outwards beneath the ectodermal. This view has not been supported by later observers (Kerr, 840 ; Jacobshagen, 786).

But, while it may be considered as established that the gill-lamellae of all Gnathostomes are generally and probably always covered by ectoderm, and are homologous organs, there remains considerable doubt with regard to those of the Cyclostomes. In this group, as already explained, they are situated more deeply on the inner region of the gill-bars and would appear to develop within the endodermal area.[1]

On this account a sharp distinction is sometimes drawn between the 'endobranchiate' Cyclostomata and the 'ectobranchiate' Gnathostomata (Goette, 783 ; Sewertzoff, 701).

[1] Nevertheless, the evidence on this point is still uncertain ; further investigation may well show that even here there is an early ingrowth of ectoderm, and that the gill-lamellae of Cyclostomata are wholly homologous with those of Pisces (see p. 496).

CHAPTER X

VASCULAR SYSTEM AND HEART

THE VASCULAR SYSTEM OF THE HEAD AND BRANCHIAL REGION

General Plan of the Vascular System.—No description of the gills and gill-bars would be complete without an account of their blood-vascular supply. The general plan of the vascular system of a primitive Craniate is as follows. The venous blood of the alimentary canal (stomach and intestine) is collected into a median longitudinal

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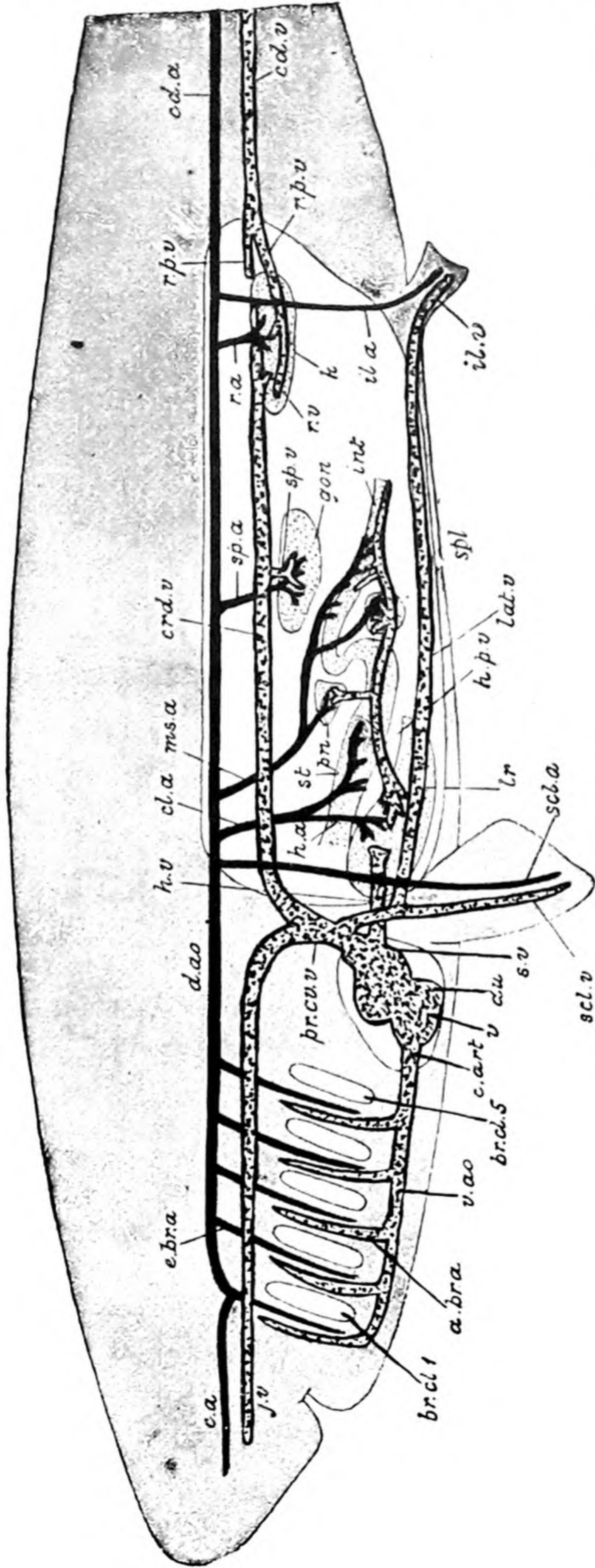subintestinal vein passing forwards to the liver where it breaks up

FIG. 530.

Diagram of the vascular system of a fish. Vessels containing aerated blood red; those containing non-aerated blood blue.** *a.br.a*, Afferent branchial artery; *au*, atrium; *br.cl*, 1-5, branchial clefts; *c.a*, carotid artery; *c.art*, conus arteriosus; *cd.a*, caudal artery; *cd.v*, caudal vein; *cl.a*, coeliac artery; *crd.v*, cardinal vein; *d.ao*, dorsal aorta; *e.br.a*, efferent branchial artery; *gon*, gonad; *h.a*, hepatic artery; *h.p.v*, hepatic portal vein; *h.v*, hepatic vein; *il.a*, iliac artery; *il.v*, iliac vein; *int*, intestine; *j.v*, jugular vein; *k*, kidney; *lat.v*, lateral vein; *lv*, liver; *ms.a*, mesenteric artery; *pn*, pancreas; *pr.cv.v*, pre-caval vein; *r.a*, renal artery; *r.p.v*, renal portal vein; *r.v*, renal vein; *scl.a*, subclavian artery; *scl.v*, subclavian vein; *sp.a*, spermatic artery; *spl*, spleen; *sp.v*, spermatic vein; *st*, stomach; *s.v*, sinus venosus; *v*, ventricle; *v.ao*, ventral aorta. (From Parker's *Elementary Biology*.)

*Instead of red, black.

**Instead of blue, coarsely stippled.

into a network of small vessels. These join again to form the hepatic veins carrying the blood to the posterior chamber of the heart or sinus venosus. The venous blood from in front of the heart is collected by cerebral and segmental veins from the head and body-wall into paired longitudinal anterior cardinal veins, and that from behind the heart by segmental veins into paired longitudinal posterior cardinal veins. The latter receive venous blood from the tail, body-wall, kidneys, limbs, etc. On either side the anterior and posterior cardinals, running dorsally to
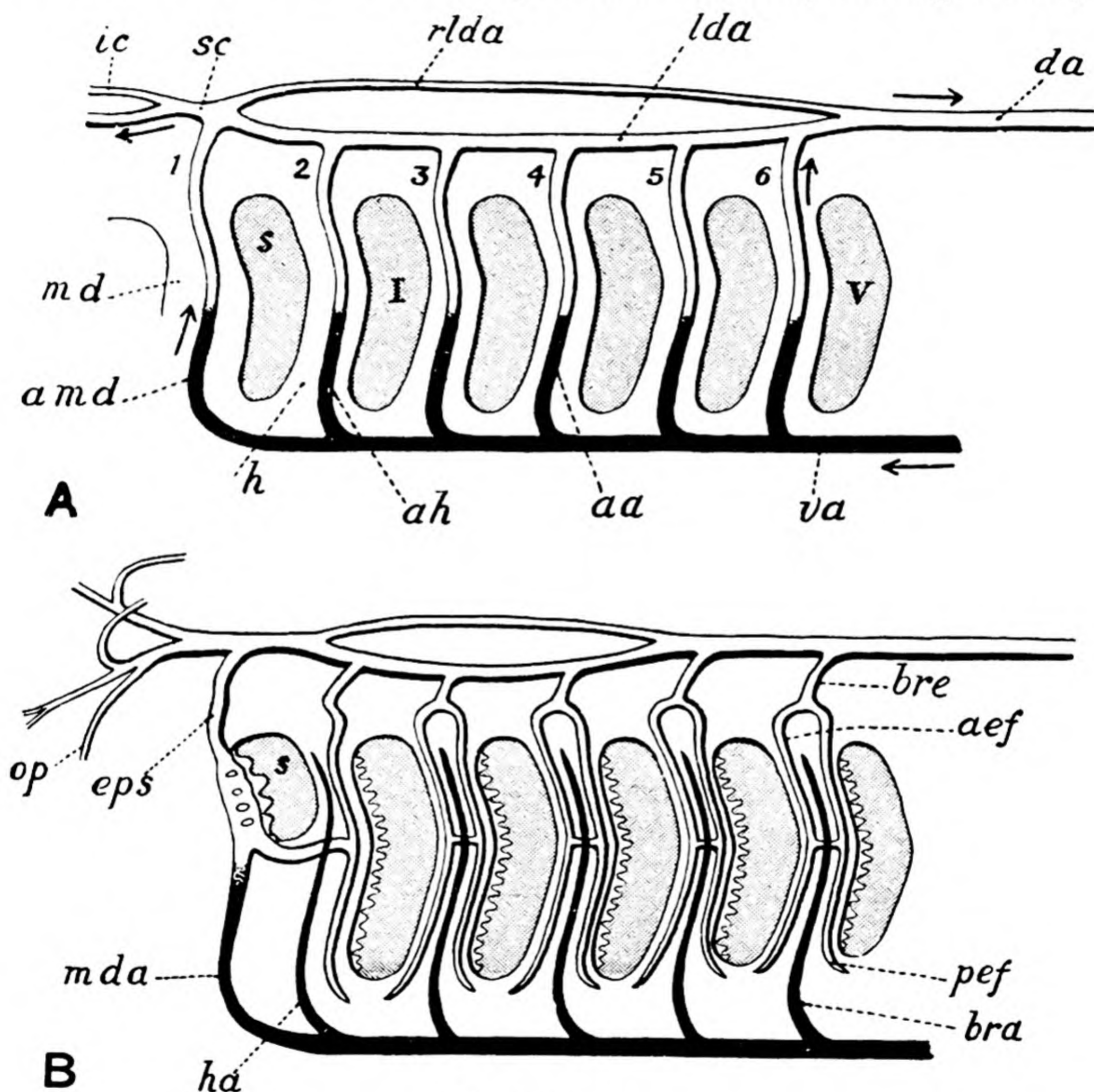

FIG. 531 A, B.

Diagrams illustrating development and fate of primitive embryonic arterial arches in a *Selachian*: left-side view completed. Afferent branchial vessels black, efferent vessels and other arteries white. (Partly from works of Dohrn, Allis, de Beer, and Sewertzoff.) A, Earliest stage; C, latest stage. 1-6, Primitive arches; *I-V*, branchial gill-slits; S, spiracular slit *aef*, Anterior efferent; *ah*, afferent of hyoid bar; *amd* and *mda*, afferent of mandibular bar; *aps*, afferent pseudobranchial cross anastomosis; *bra*, afferent branchial vessel; *bre*, epibranchial artery; *ce*, cerebral; *co*, cross

the coelom below the notochord, meet to form a ductus Cuvieri which passes across by the septum transversum to the sinus venosus. Moreover,

in the Dipnoi and Tetrapoda, the venous blood from the posterior region
of the body-wall and from the kidneys is diverted into a new vein, the
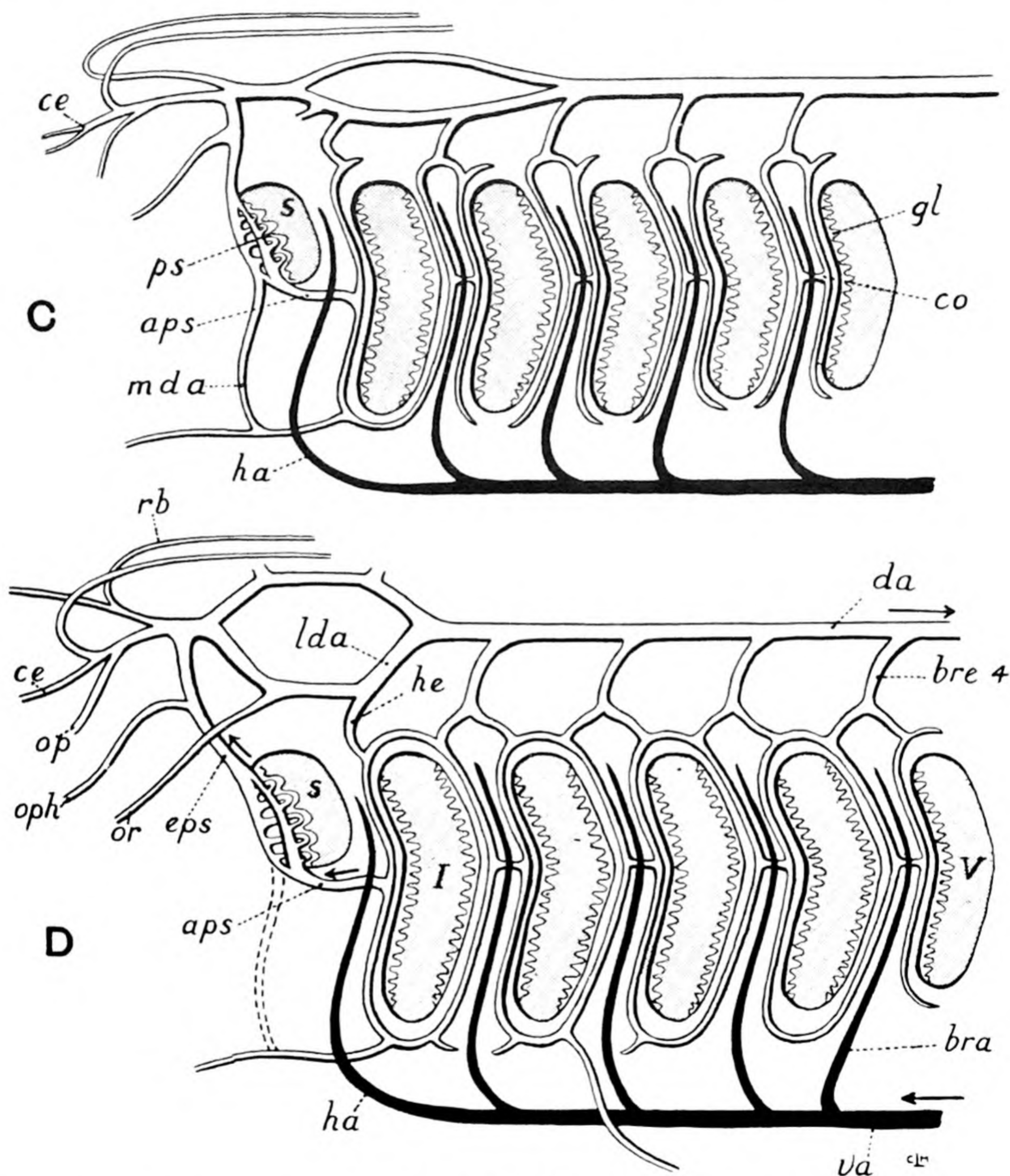

FIG. 531 C, D.

commissural vessel; *da*, median dorsal aorta; *eps*, efferent pseudobranchial (dorsal part of 1);
gl, gill-lamellae; *h*, hyoid bar; *ha*, afferent, and *he*, efferent vessel of hyoid bar; *ic*, internal carotid;
lda, left lateral dorsal aorta; *md*, mandibular bar; *mda*, its vascular arch; *op*, optic; *oph*,
ophthalmic; *or*, orbital; *pef*, posterior efferent; *ps*, mandibular pseudobranch; *rb*, posterior
cerebral; *rlda*, right lateral aorta; *sc*, sinus cephalicus; *va*, ventral aorta.

vena cava inferior, passing downwards and forwards through the liver
to join the hepatic veins and open into the sinus venosus. Thus in all

Craniata the venous blood from both the splanchnic and somatic systems reaches the heart and is pumped forward along a median longitudinal ventral aorta which bifurcates behind the thyroid gland. The ventral aorta gives off at intervals paired aortic arches which run up the visceral arches to join the longitudinal dorsal aorta, Fig. 530.

The aorta develops from paired rudiments which fuse below the notochord to a median dorsal aorta behind, but remain to a varying extent separate in the branchial region and head. The aorta distributes oxygenated 'arterial' blood to the body generally, including the head region, limbs, alimentary canal, kidneys and gonads, and gives off paired segmental arteries to the body-wall all along its course. All the vessels carrying blood to the heart are called veins, and all the vessels carrying blood away from the heart to all parts of the body are called arteries. The blood passes from the arterial system to the venous by minute capillary vessels.

The Aortic Arches in Cyclostomes and Fishes.—There are developed six pairs of primary aortic arches, one in front of each visceral cleft, in the embryo of all Craniata (with the exception of the Cyclostomes and Selachians with a larger number of visceral clefts, in which an additional arch occurs for each slit). But of these six, the second in the hyoid bar, and especially the first in the mandibular bar, become greatly modified, as will be explained later (p. 514).

It is important to notice that in Dipnoi, *Polypterus*, and *Amia* the so-called air-bladder is supplied by a 'pulmonary artery' from the last epibranchial artery (sixth aortic arch) as in all Tetrapods (see p. 583).

In all the gill-bearing visceral arches of Pisces the primary aortic arch becomes interrupted in such a way that the blood has to filter through the gill-lamellae where it is oxygenated, Fig. 533. Afferent and efferent branchial vessels are thus formed, the former bringing venous blood from the ventral aorta, the latter taking arterial blood to the dorsal aorta, and the two communicate only by a system of delicate loops in the lamellae of the gills. Goette (782-3) showed that the development of the afferent and efferent vessels takes place differently in Elasmobranchs and in Teleostei; the greater part of the original arch forming the afferent vessel in the first group and the efferent vessel in the second.

In all Pisces the afferent vessel passes up the bar outside the efferent vessel, and the skeletal arch lies inside all these vessels. In each bar the afferent vessel is always single in Teleostei; but in Elasmobranchs and Dipnoi there are two efferent vessels, one to each row of lamellae, Fig. 525. Moreover, the dorsal efferent arteries (epibranchial arteries) of adult Selachii owing to secondary shifting correspond no longer to their

gill-bars but to the gill-slits (p. 514), whereas in other fishes they retain their original position.

In the embryonic branchial bar of a Selachian (Goette, 783 ; Dohrn, 333 ; Sewertzoff, 869) the anterior and posterior efferent branchial vessels develop separately parallel to the primary continuous aortic arch with which they become connected by capillary loops ; the primary arch then becomes interrupted dorsally and its longer ventral portion is converted into the afferent vessel. The newly formed efferent vessels having joined the shorter dorsal portion, this now functions as the epibranchial artery carrying oxygenated blood to the dorsal aorta (about

FIG. 532.

Diagram of branchial circulation of *Selachian*, left-side view completed.   *at*, Atrium ; *ba*, basal artery ; *c*, conus ; *ca*, cardiac ; *cae*, coeliac ; *dc*, ductus Cuvieri ; *hbr*, hypobranchial ; *he*, posterior efferent of hyoid bar ; *hv*, hepatic veins ; *scl*, subclavian ; *v*, ventricle.   Other letters as in Fig. 531.

the middle of the bar transverse connexions early arise between the two efferent vessels). A transverse section of the branchial bar of an Elasmobranch, then, shows two inner efferent vessels, each joined to the single outer afferent vessel by a series of loops passing into the lamellae, Figs. 517, 533. The transverse section of a Teleostean gill-bar, however, shows only two branchial vessels, an outer afferent and an inner efferent, connected by a double series of loops passing into the anterior and posterior gill-lamellae. In development it is found that here the primitive aortic arch is interrupted near its ventral base, and that while the greater part of the arch is converted into the efferent branchial vessel, the afferent vessel is a new formation joined to the base of the aortic arch. There is thus an important difference between the gill-vessels of these two groups of fishes ; but intermediate conditions occur in the lower Teleostomes. In *Acipenser* the upper region of the gill-bar conforms to the Teleostean

and the lower to the Elasmobranch type. The aortic arch is here inter-
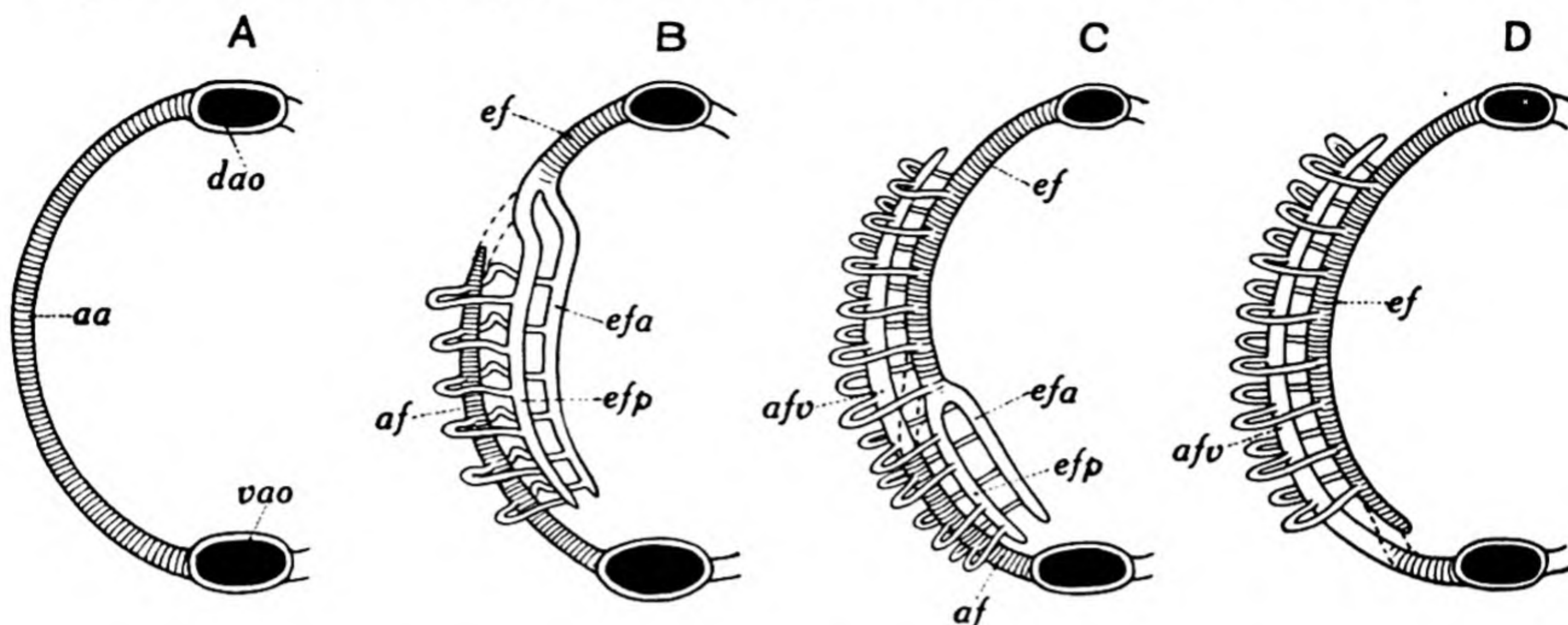rupted about half-way; its dorsal portion is continued ventrally into

FIG. 533.

Diagrams illustrating development of adult branchial vessels in various fishes. A, Original
continuous embryonic arch cross-lined; B, Selachian; C, intermediate form such as *Acipenser*; D,
Teleost. Newly developed vessels, white. In B, C, D original arch interrupted. *aa*, Embryonic
vascular arch; *af*, afferent; *afv*, newly formed afferent; *dao*, dorsal aorta; *ef*, efferent epibranchial;
efa, anterior efferent; *efp*, posterior efferent; *vao*, ventral aorta; small loops pass in branchial
lamellae from afferent to efferent vessels.

two newly formed efferent vessels, and its ventral portion is prolonged
upwards to complete the afferent vessel, Fig. 533 (Sewertzoff, 869). A
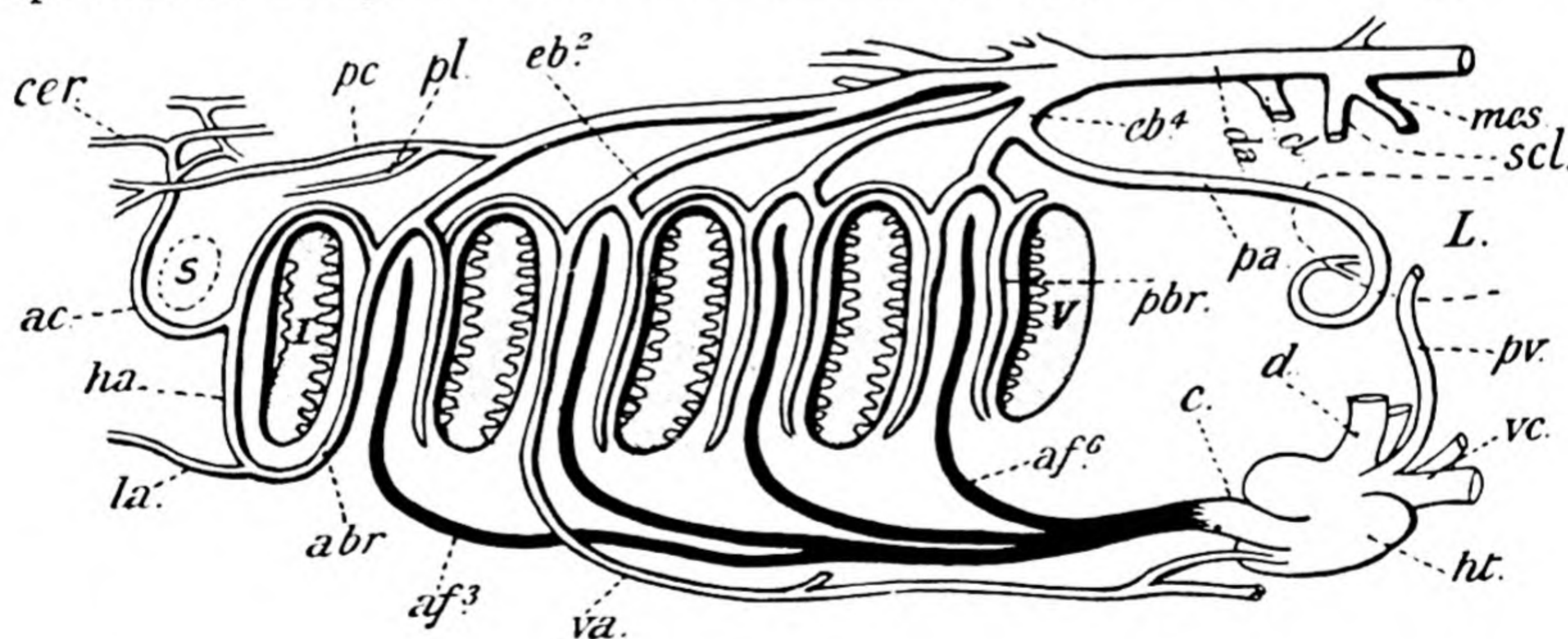
FIG. 534.

Diagram of branchial circulation of *Ceratodus forsteri* (chiefly from W. B. Spencer, 1892). *I-V*,
Five branchial slits with gill-lamellae. *abr*, Anterior efferent vessel of first branchial bar; *ac*, efferent
'pseudobranchial', portion of mandibular; *af³-⁶*, afferent vessels of four branchial bars, correspond-
ing to original aortic arches 4-6; *c*, conus; *cer*, cerebral artery; *cl*, coeliac artery; *d*, left ductus
Cuvieri; *eb²* and *eb⁴*, second and fourth epibranchial arteries; *ha*, hyoid artery, derived from second
aortic arch; *L*, lung (air-bladder); *la*, lingual artery; *mes*, mesenteric artery; *pa*, left pulmonary
artery; *pbr*, posterior efferent artery of fourth branchial bar; *pc*, orbital artery; *pl*, palatine artery;
pv, pulmonary vein; *s*, position of closed spiracle; *scl*, subclavian artery; *va*, hypobranchial artery.

similar disposition is found in *Lepidosteus* and in *Amia*, where a second
(posterior) efferent artery also occurs dorsally (Allis, 806).

Since the gill-bearing bars of Dipnoi are also provided with an outer

afferent and two inner efferent vessels (Spencer, 872 ; Kellicott, 789 ; Parker, 854), this would appear to be an ancient disposition preserved in both the Chondrichthyes and the primitive Osteichthyes, from which the Teleostomes have diverged owing to a progressive tendency for the aortic arch to become converted into the efferent vessel, Fig. 534.

It may here be mentioned that in *Protopterus* the three pairs of external gills are supplied from the vessels of the last three pairs of gill-bars (fourth, fifth, and sixth aortic arches). The third and fourth aortic
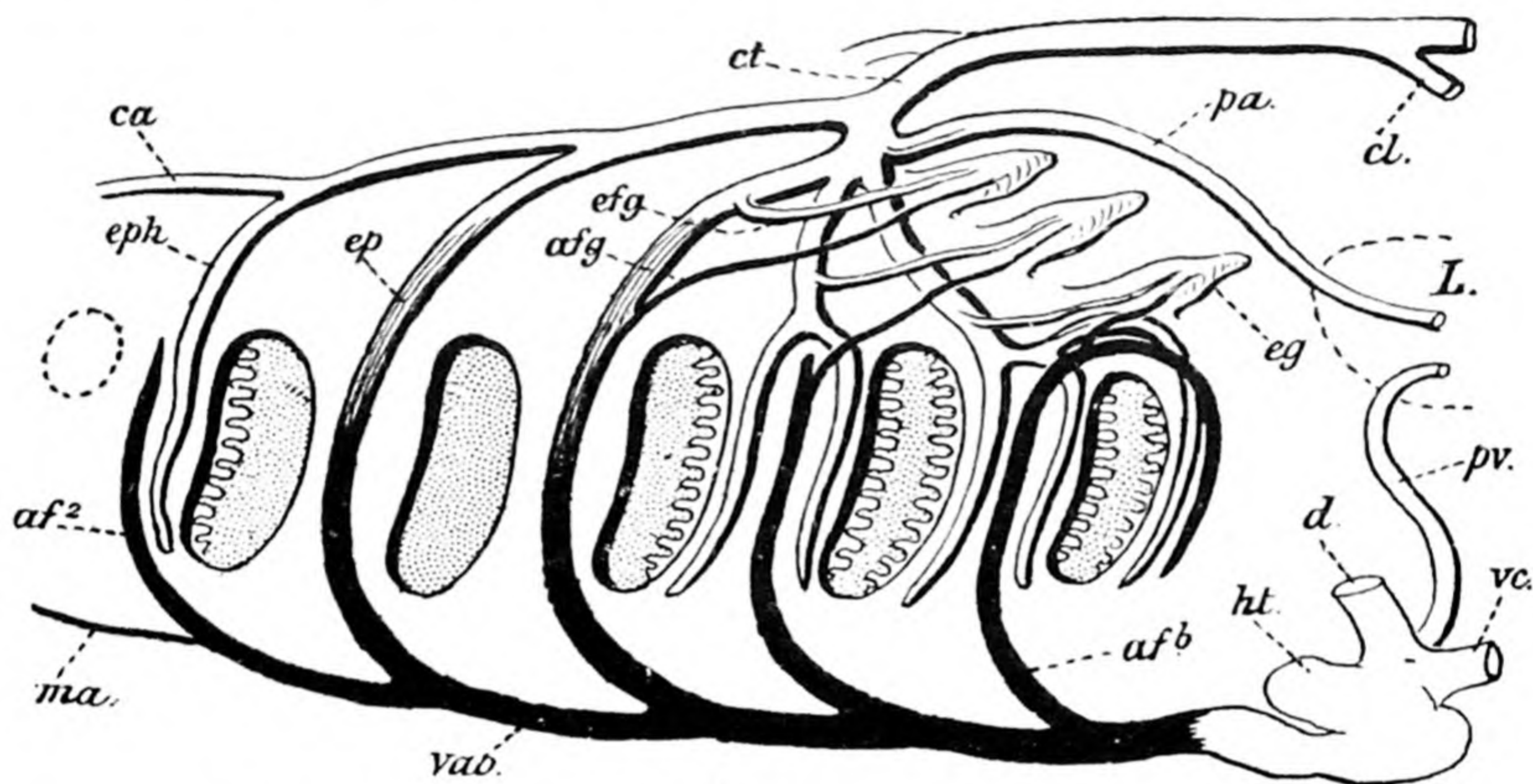
FIG. 535.

Branchial circulation of *Protopterus* (from Parker's figures). *af*[2-6], Afferent branchial arteries ; *afg*, afferent vessel to external gill ; *ca*, carotid ; *cl*, coeliac artery ; *ct*, left branch of dorsal aorta formed by junction of branchial efferent vessels ; *d*, ductus Cuvieri ; *efg*, efferent vessel of external gill ; *eg*, external gill ; *ep*, epibranchial region of arterial arch of first gill-less branchial arch ; *eph*, epibranchial vessel of hyoid arch ; *ht*, heart ; *L*, lung ; *ma*, lingual artery ; *pa*, pulmonary artery ; *pv*, pulmonary vein ; *vao*, ventral aorta ; *vc*, vena cava posterior. The five branchial slits are shaded ; the first two branchial arches are without gills. A dotted line indicates the position of the obliterated spiracle.

arches of *Protopterus* remain as continuous vessels running from the ventral to the dorsal aorta in the first and second branchial bars which have lost their gills, Fig. 535. This resemblance to the Amphibian structure is probably due to convergence, since it is not shown by *Ceratodus*. Other resemblances to the Amphibia in the arterial system of the Dipnoi, such as the gathering of the epibranchial arteries on each side before they unite to form the aorta and the shortening of the ventral aorta to form a truncus with subdivided lumen, seem to indicate true affinity with the lower Tetrapods (see also p. 552).

In all fishes the efferent branchial vessels tend to anastomose ventrally below the gill-slits, giving rise to more or less continuous vessels from which arise hypobranchial arteries supplying the ventral branchial region

and the heart. Similar dorsal anastomoses occur above the gill-slits from posterior to anterior efferent vessels in *Ceratodus* and Selachii (Parker, 853 ; Spencer, 872).

The secondary shifting in Selachians of the epibranchial artery, mentioned above, takes place owing to its thus acquiring a connexion with the posterior efferent vessel of the bar in front and then losing the earlier connexion with the anterior efferent of its own bar ; the epi-branchial artery now receives blood from the anterior and posterior hemibranchs of one slit (Dohrn, 333 ; Sewertzoff, 869). It is interesting to note that in *Chlamydoselachus* the original connexions are retained in the adult (Allis, 804), Figs. 531-2, 536.

THE ARTERIAL SUPPLY OF THE FIRST TWO VISCERAL ARCHES AND HEAD IN PISCES

As was mentioned above, the originally continuous aortic arches of the embryonic mandibular and hyoid bars become greatly modified in the course of development. The divergence in fate of these and the more posterior aortic arches is partly due to the fact that the stream of arterial blood tends to become subdivided into two : the bulk of oxy-genated blood needed to supply the trunk, limbs, and tail flows backwards in the median dorsal aorta ; but there is also a no less important stream flowing forward to supply the head, and this in fishes is derived to a considerable extent from the first two aortic arches.

The fundamental relations of the internal carotids in Craniates are as follows : the lateral dorsal aortae run forwards below the basis cranii to enter the cranial cavity on either side of the pituitary body through the median foramen hypophyseos between the posterior ends of the tra-beculae cranii, Figs. 247, 271.[1] In fishes the name ' internal carotid ' is generally applied to that region of the vessel beyond the origin of the orbital artery (external carotid of some authors). The ' internal carotid ' of Tetrapods reaches down to its origin with the true external carotid from the ventral 'common carotid ' (ventral aorta).

Whether the true forward continuations of the lateral dorsal aortae are represented by the internal carotids, or, as suggested by Allis, by orbito-nasal arteries running forwards through the orbits in some Teleo-stomes, is doubtful. The true external carotids are considered in Tetrapods

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[1] A few exceptions occur among fishes (*Polypterus*, *Amiurus*, Allis, 410, 803) and Amphibia (Anura), in which the internal carotid appears to enter the side wall of the brain-case farther forwards ; but they are probably always due to secondary modifications—the establishment of a lateral vessel and obliteration of a portion of the original internal carotid, as Gaupp showed in *Rana* (504). See also Mammalia, p. 263.

to be the forward continuations of the ventral aorta,[1] and are represented in fishes by small branches of the hypobranchial arteries and vestigial
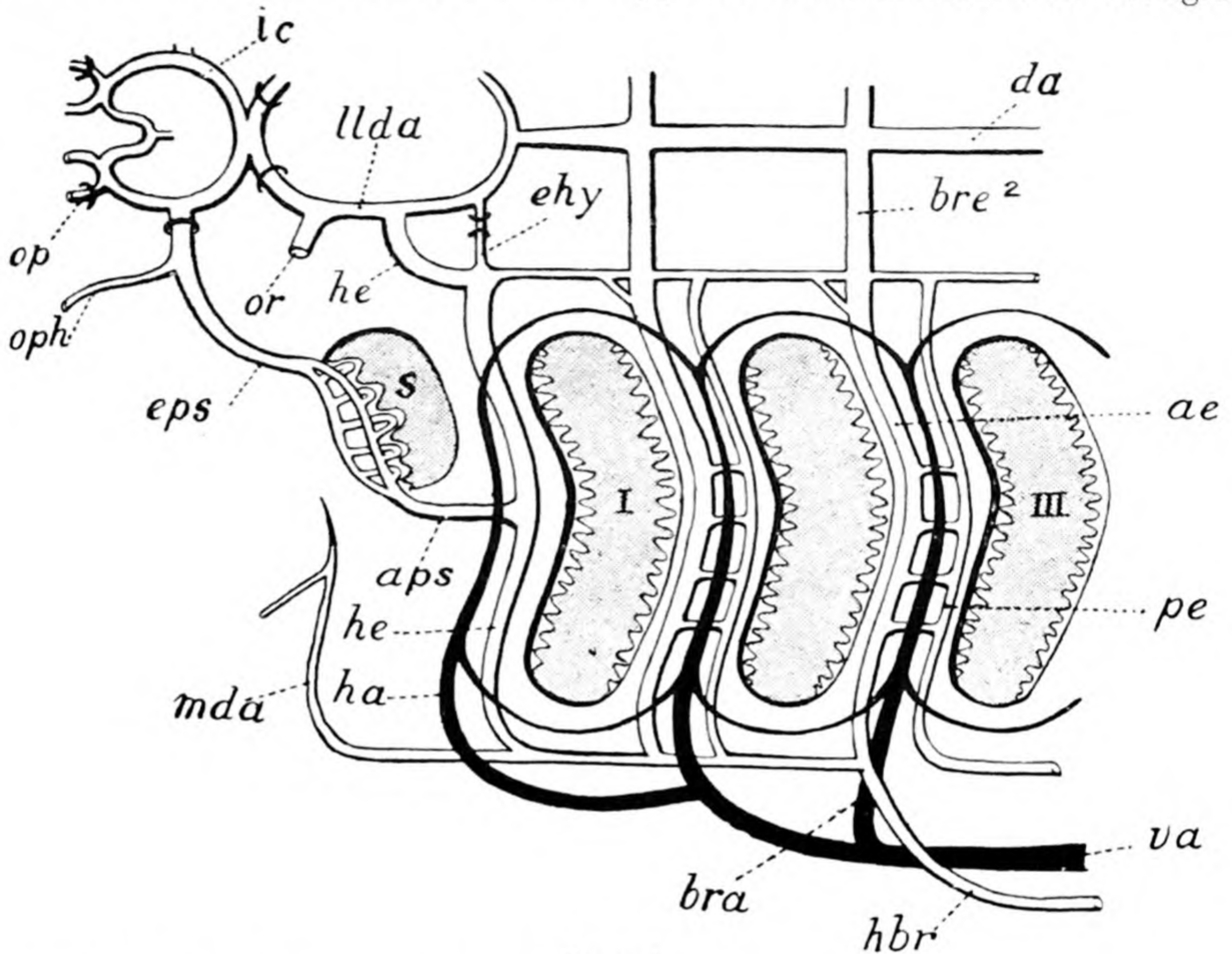

FIG. 536.

Chlamydoselachus anguineus: diagram of cerebral and anterior branchial circulation (modified from Allis, 1911). *bre²*, Epibranchial of 2nd branchial bar; *ehy*, epibranchial of hyoid bar. Other letters as in Fig. 532.

ventral part of the mandibular arch to the thyroid gland and region of the lower jaw.

In Pisces the internal carotid gives off intracranially ophthalmic, optic, and cerebral arteries, the two former passing out of the cranial cavity

[1] There is considerable confusion in the nomenclature of the arteries of fishes. For the convenience of the reader the following synonyms may be given : Orbital artery (Carazii) =carotis facialis (Rathke), external carotid (Allis, and others), posterior carotid (T. J. Parker), art. temporalis (Greil). Ophthalmic artery =art. ophthalmica magna, art. choroidalis (Dohrn), art. orbitalis (Greil). Optic artery (Allis) =art. centralis retinae (Dohrn), art. ophthalmica minor (Müller), art. ophthalmica (Greil). Afferent mandibular vessel =art. hyoidea (Wright), art. pseudobranchialis (Parker), art. thyreo-spiracularis and part of afferent spiracular (Dohrn). Efferent pseudobranchial vessel (Allis) =anterior carotid (Parker), part of afferent spiracular and carotis interna anterior (Dohrn). The common carotid of T. J. Parker is that part of the lateral dorsal aorta between its bifurcation into posterior and internal carotids and its junction with the efferent hyoidean vessel.

dorsally to the trabecula. The important orbital artery comes off the lateral dorsal aorta close to the second aortic arch (or from this arch) ventrally to the basis cranii, Figs. 532, 537-8. It does not enter the cranial cavity, but may pierce the subocular shelf or pass through the jugular canal (p. 276).

Selachii.—Of the many works on the arterial system of the Selachii one may mention those of Hyrtl (1858 and 1871), T. J. Parker (853), Ayers (807), Allis (804), Carazzi (818), on its anatomy ; and of Dohrn (333),
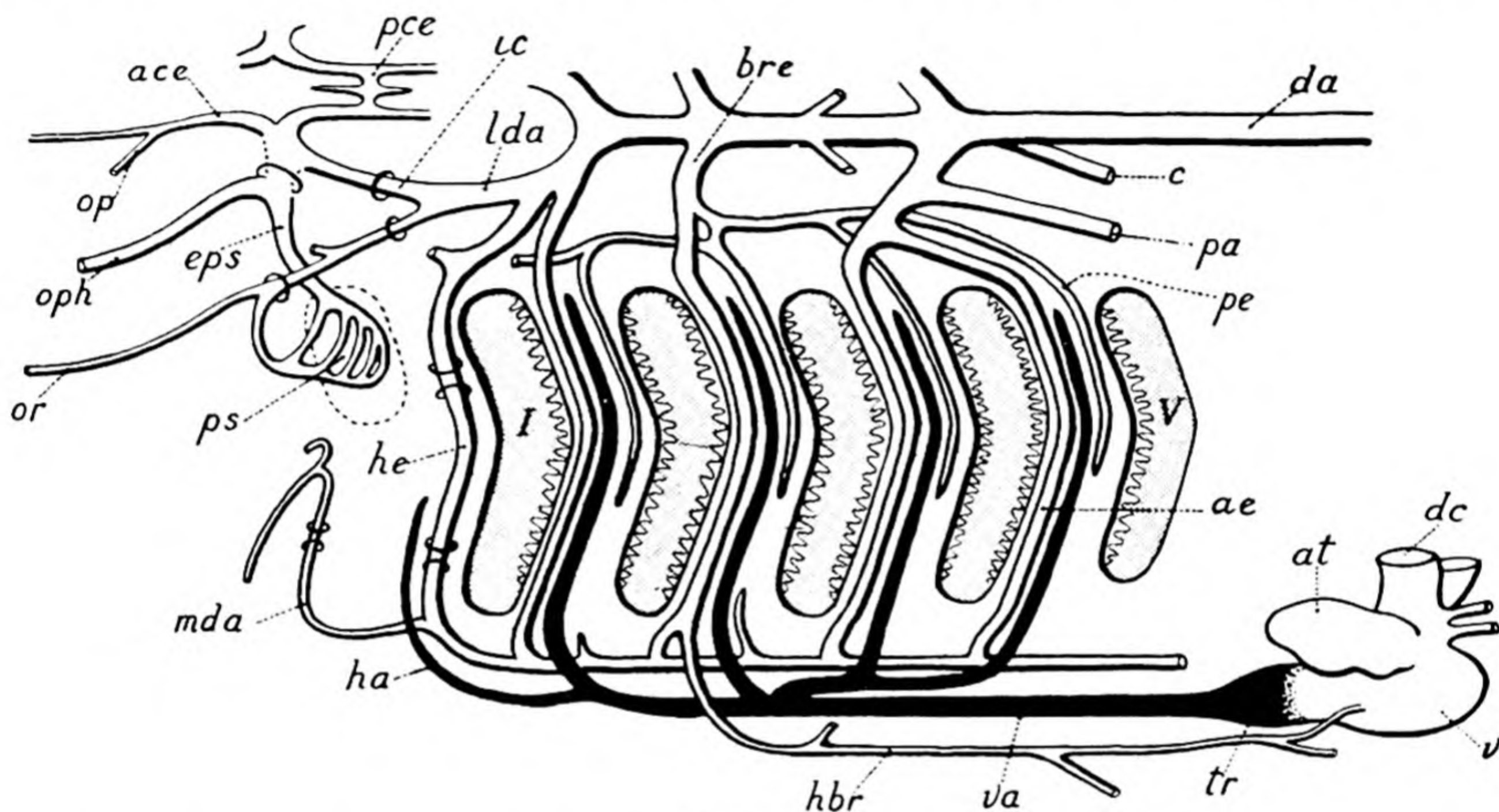
FIG. 537.

Amia : branchial circulation, left-side view completed (modified from Allis, 1912). *ace*, Anterior cerebral ; *pce*, posterior cerebral ; *pa*, pulmonary artery. Other letters as in Figs. 531 and 532.

Rückert (863), Platt (855), Raffaele (856), Scammon (380), de Beer (421), on its development.

The second or hyoidean aortic arch is soon interrupted, giving rise, as in the branchial bar, to an afferent vessel from the ventral aorta and a dorsal epibranchial vessel. Since only a posterior hemibranch is present only one corresponding efferent branchial vessel is developed in the hyoid bar. Very early the first or mandibular aortic arch becomes connected with the hyoidean efferent vessel by a commissural vessel below the spiracular slit. The mandibular aortic arch then becomes interrupted ventrally to this connexion, and its ventral portion secondarily united to the lower end of the efferent hyoidean vessel or anterior end of the hypobranchial artery ; it supplies in the adult the thyroid gland and lower jaws. As soon as the mandibular pseudobranch develops, the mandibular aortic arch divides into capillaries to supply its lamellae

above the point where it receives the commissural vessel. The latter now functions as the afferent pseudobranchial vessel receiving arterial blood from the hyoidean efferent vessel. The more dorsal remainder of the mandibular aortic arch becomes the efferent pseudobranchial vessel which joins the lateral dorsal aorta (internal carotid), Figs. 531-2, 536. It is a remarkable fact, discussed elsewhere, that in Selachians alone this efferent vessel passes in to join the internal carotids dorsally instead of ventrally to the trabecula cranii (p. 529).

The lateral dorsal aortae unite in a median sinus cephalicus ventral to the tip of the notochord in the very early embryo, Fig. 234, and this union persists in the adult forming the anterior limit of a circulus cephalicus passing behind the pituitary body.[1] From the sinus spring the internal carotids, which receive the efferent pseudobranchials and give off optic and cerebral arteries. Intracranial branches of the latter meet below the brain to form the median basilar artery. The orbital artery, supplying the orbit, side of the head, and jaws, arises from the lateral dorsal aorta close to its junction with the efferent hyoidean vessel. The anatomical relations of the chief arteries are explained elsewhere (p. 528).

Teleostomi.—Where the hyoidean hemibranch persists, as in *Lepidosteus*, an afferent vessel supplies it from the ventral aorta ; but this vessel disappears in *Acipenser* where the hemibranch is a ' pseudobranch ' receiving only arterial blood, and also in other forms without a hyoidean hemibranch except *Amia* (Allis). As in Selachians the afferent mandibular vessel becomes secondarily connected to the hypobranchial arterial system ; it is retained in Chondrostei, *Lepidosteus*, and some Teleosts (*Gadus*), Fig. 539, but is usually interrupted before reaching it. The cross commissural vessel from the hyoidean to the mandibular arch seems to be always developed in the embryo, though it may disappear later (*Amia* and most Teleosts). The pseudobranch then receives its arterial blood from the mandibular arch (if complete) and a branch of the orbital artery which anastomoses with it (Allis). The efferent hyoidean and orbital arteries may be much developed to supply the opercular region. Optic, ophthalmic, and orbital arteries occur ; but the ophthalmic disappears when the chorioidal gland is absent (*Lepidosteus, Polypterus, Amiurus*). In connexion with this chorioidal gland, the name given to a rete mirabile on the eye-ball, it should be mentioned that Dohrn and Allis consider that it represents the vestige of a premandibular gill comparable to the pseudobranch of the mandibular arch. The existence, however, of a premandibular gill-slit has not yet been proved in any Craniate (p. 448).

[1] A circulus cephalicus is also completed behind the hypophysis in Dipnoi, and persists in the adult (Spencer, 872).

A characteristic feature of the Teleostei is the formation of a circulus cephalicus due to the reunion inside the skull of the divergent lateral dorsal aortae, Figs. 288-9, 538. Already in *Amia* the efferent pseudobranchial tends to separate from the internal carotid and pass directly into the ophthalmic artery. The dorsal connexion with the carotid is obliterated, at all events in some individuals (de Beer, **421**). In Teleosts this is the usual definitive condition; the two internal carotids come close together and fuse to complete the circulus cephalicus, while the separated
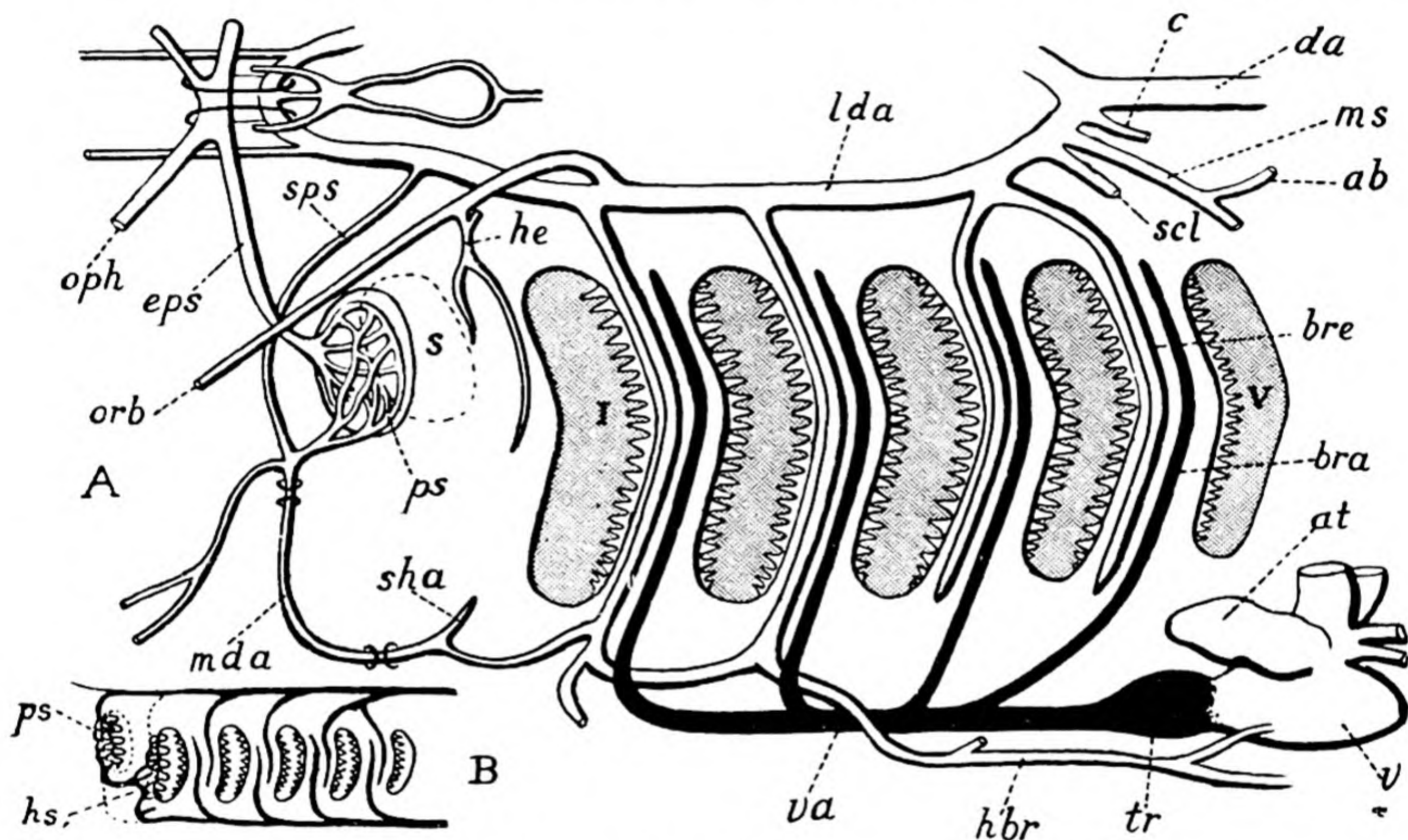
FIG. 538.

A, *Gadus*: branchial circulation, left-side view completed (modified from Allis, 1912). B, Branchial circulation of *Lepidosteus*. *ab*, Branch to air-bladder; *ms*, mesenterial; *s*, position of closed spiracle; *sha*, secondary afferent hyoidean; *sps*, secondary afferent pseudobranchial artery; *tr*, bulbus. Other letters as in Figs. 531-2.

efferent pseudobranchial arteries continue forwards as the ophthalmics. A slender cross vessel also unites them in front of the circulus. Both these unions across the middle line are secondary and anterior to the pituitary body, and are therefore not homologous with the sinus and circulus of the Selachian (Allis, **807**).

The extent of the circulus cephalicus varies greatly in Teleosts, owing to the lateral dorsal aortae being more or less completely fused: in *Gadus* it is extensive and receives all four pairs of epibranchial arteries; in *Clupea* it is much reduced and receives only the first pair (Ridewood, **680**).

THE PSEUDOBRANCH AND ITS VASCULAR SUPPLY

The Spiracle and Pseudobranch.—We may now return to the consideration of the first gill-slit in the Gnathostomata. Even when it is widely open in the embryo, as in Elasmobranchs, this spiracular slit is always more or less completely closed in the adult. The closure takes place from its ventral end, and its dorsal region only may remain open. It occurs in Selachii as a small dorsal pouch passing outwards from the pharynx between the mandibular and hyoid arches, and usually opening behind the eye by a small pore or spiracle. While it is minute or even closed in
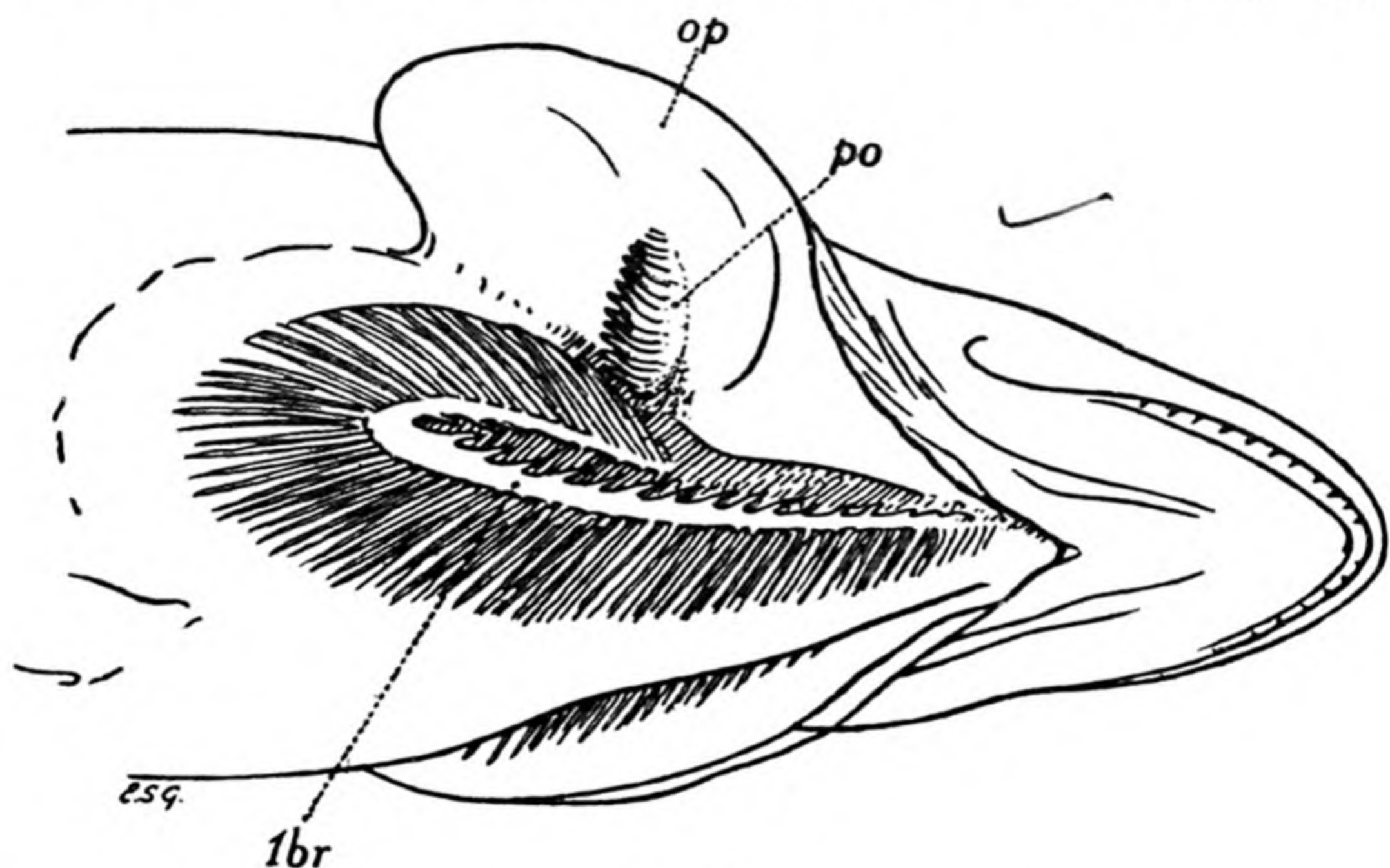
FIG. 539.

Ventro-lateral view of head of *Salmo salar* with right operculum, *op*, raised to show first branchial arch, *ıbr*, and pseudobranch, *po*.

some Lamnidae and Carchariidae, the spiracle is larger in Spinacidae, and largest in Rajiformes, where it is provided on its anterior wall with a movable valvular flap strengthened by the prespiracular cartilage, Fig. 440. In these bottom living fish it may serve, when the mouth is applied to the ground, for the passage in and out of a current of water for respiration. On the front wall of the spiracular slit is the pseudobranch (p. 516).

The adult Holocephali and Dipnoi have lost both pseudobranch and spiracular slit; but in Teleostomes an open spiracle persists in Polypterini, *Acipenser*, and *Polyodon*. In all other adult Teleostomes the spiracle is closed, although a distinct vestige may remain of the pharyngeal pouch in *Amia, Lepidosteus*, and some Teleosts (Wright, 882; Sagemehl, 378). A pseudobranch is here developed in *Acipenser, Polyodon, Lepidosteus, Amia*, and the majority of Teleosts, Figs. 537-9.

These pseudobranchs have attracted much attention, and have been studied by many observers since they were first discovered as a pair of gill-like organs on the inner surface of the opercular fold in Teleosts by Broussonet in 1782. The two pairs of subopercular gills (pseudobranchial and opercular hemibranchs) of *Acipenser* were later found by v. Baer (1827), and those of *Lepidosteus* by Valentin (1831). It was Hyrtl (1838) who first pointed out that the pseudobranch is supplied with arterial blood and therefore is not respiratory in function. In 1839 J. Müller gave a masterly account of these organs in Pisces, established the homology of the pseudobranch of Teleostomes with that of Selachians (spiracular or posterior mandibular hemibranch), and described two kinds of Teleostean pseudobranch, (1) free, with gill-lamellae projecting into the subopercular cavity, and (2) glandular, sunk below a covering epithelium. He suggested that the pseudobranch regulates the pressure of the blood supplied to the chorioid gland of the eye, since the afferent artery breaks up into capillaries which unite again to form the efferent pseudobranchial artery from which comes off the great ophthalmic artery.

Recently our knowledge of the pseudobranch has been greatly increased by the researches of Granel (827-30) and Vialli (880-81), who have described special secretory ' acidophil cells ' in the higher forms. The Selachii (except *Scymnus*) possess a well-developed gill-like pseudobranch (mandibular hemibranch) lodged in the spiracular slit and reaching to near its external opening. Its lamellae may be numerous but bear few secondary lamellae, and these are thick and covered by a thick epithelium of cubical cells. The vascular tissue at the base seems to have a haematopoietic and haemolytic function. There are no acidophil cells (Vialli). The pseudobranchs of *Acipenser* and *Polyodon* are of similar structure, but more deeply set in the spiracular slit. In *Lepidosteus*, where this slit is closed externally but widely open internally, the pseudobranch migrates in development into the branchial cavity to a position on the under surface of the operculum. In *Amia* the pseudobranch grows and bulges outwards on the wall of a saccular diverticulum of the spiracular slit Fig. 733. Although modified, it preserves the essential gross structure of a gill with lamellae supported by branchial rays as in the previously described forms, but, it is important to notice, resembles that of Teleosts in the appearance of a layer of acidophil cells. In the Teleostei the spiracle closes early, the mandibular pseudobranch arises near the interna opening of the spiracular slit, Fig. 529, but migrates and spreads into the subopercular cavity (Dohrn, 780).[1] It is at first a ' free ' gill-like

[1] The view that the pseudobranch of Teleosti is a hyoidean gill (Cole, 1901) lacks good evidence.

organ with projecting vascular lamellae provided with secondary lamellae, but tends to sink below the covering epithelium and lose its primitive structure in later stages in more specialised cases (Maurer, 848).

Four adult types may be distinguished (Granel, 829) : (1) a 'free' pseudobranch with lamellae set along an axis and bearing secondary lamellae all covered by ectodermal epithelium (*Trachinus*, and many other genera) ; (2) the lamellae are still free, but the epithelium covers them without sinking between the secondary lamellae (*Chrysophrys*) ; (3) the lamellae no longer project, and have sunk below the general covering of ectodermal epithelium (*Phoxinus*) ; (4) the whole organ is not only buried, but has become more or less separated from the superficial epithelium by an overgrowth of connective tissue (*Gadus*, *Cyprinus*, and others with a 'glandular' pseudobranch). Excepting for the separation from the thick ectodermal covering, the histological structure remains much the same in all four types, and may be interpreted as a modification of that of the ordinary gill with its middle vascular layer strengthened by pilaster cells, its subepithelial layer, and its now loosened ectoderm. The pseudobranch of *Amia* and the Teleostei is distinguished by the conversion of the subepithelial cells covering the middle layer into large granular secretory acidophil cells. Thus, far from being a mere useless vestigial organ, the pseudobranch seems in the higher Teleostomes to have acquired a new function, that of an endocrine gland, in addition to its original function of regulating the blood-supply to the eye. What this new endocrine action may be is not yet known.

The blood-supply to the pseudobranch is dealt with elsewhere (p. 516), but it may here be pointed out that, owing to the formation of an anastomosis (afferent pseudobranchial artery) with the efferent vessel of the hyoid arch and interruption of the ventral region of the mandibular arch, it receives only arterial blood, Figs. 532, 537-8. This is the condition in Selachians, and usually found in the lower Teleostomes, and many Teleosts (*Salmo*) ; but in *Polyodon* the ventral mandibular supply persists, and in *Gadus* is added to it a secondary afferent vessel coming from the circulus cephalicus. In *Amia* and such Teleosts as *Esox* this secondary vessel (which may be derived from the orbital artery) alone supplies blood to the pseudobranch (Hyrtl, 1858–72 ; F. W. Müller, 851 ; Maurer, 848 ; and especially Allis, 802-3, 806).

THE AORTIC ARCHES IN TETRAPODA

The fate of the aortic arches in Tetrapods affords material for one of the most instructive studies of the evolution of vertebrate structure. Among the various factors which contribute to their gradual modification
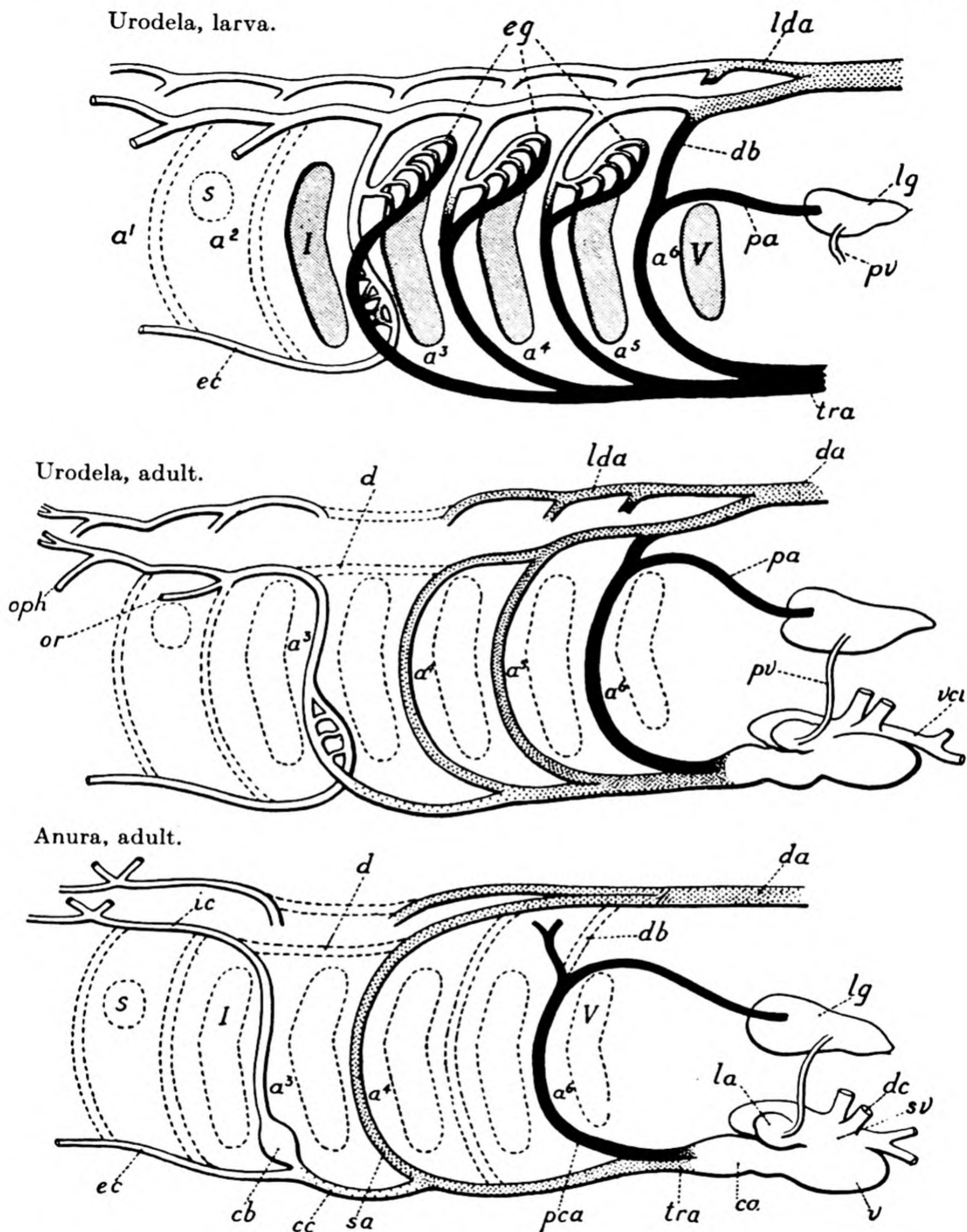
FIG. 540.

Diagrams illustrating development and fate of aortic arches in *Amphibia*, left-side view completed. Vessels carrying most arterial blood white, most venous blood black, and mixed blood stippled. a^{1-6}, Primary arterial arches ; *ca*, conus arteriosus ; *cb*, carotid gland ; *cc*, common carotid ; *da*, median dorsal aorta ; *db*, ductus Botalli ; *dc*, left ductus Cuvieri ; *ec*, external carotid ; *eg*, blood-supply to external gill ; *ic*, internal carotid ; *la*, left auricle ; *lda*, lateral dorsal aorta (*d*, obliterated part = ductus caroticus) ; *lg*, lung ; *oph*, ophthalmic ; *or*, orbital ; *pa*, pulmonary artery ; *pca*, pulmo-cutaneous arch ; *pv*, pulmonary vein ; *s*, closed spiracular slit ; *sa*, systemic arch ; *sv*, sinus venosus ; *tra*, truncus arteriosus (ventral aorta) ; *v*, ventricle ; *vci*, vena cava inferior.

may be mentioned the establishment of pulmonary and loss of branchial respiration, the increasing separation in the heart of the venous from the arterial blood-stream, and the differentiation of the neck and consequent retreat of the heart to a more posterior position in the thoracic
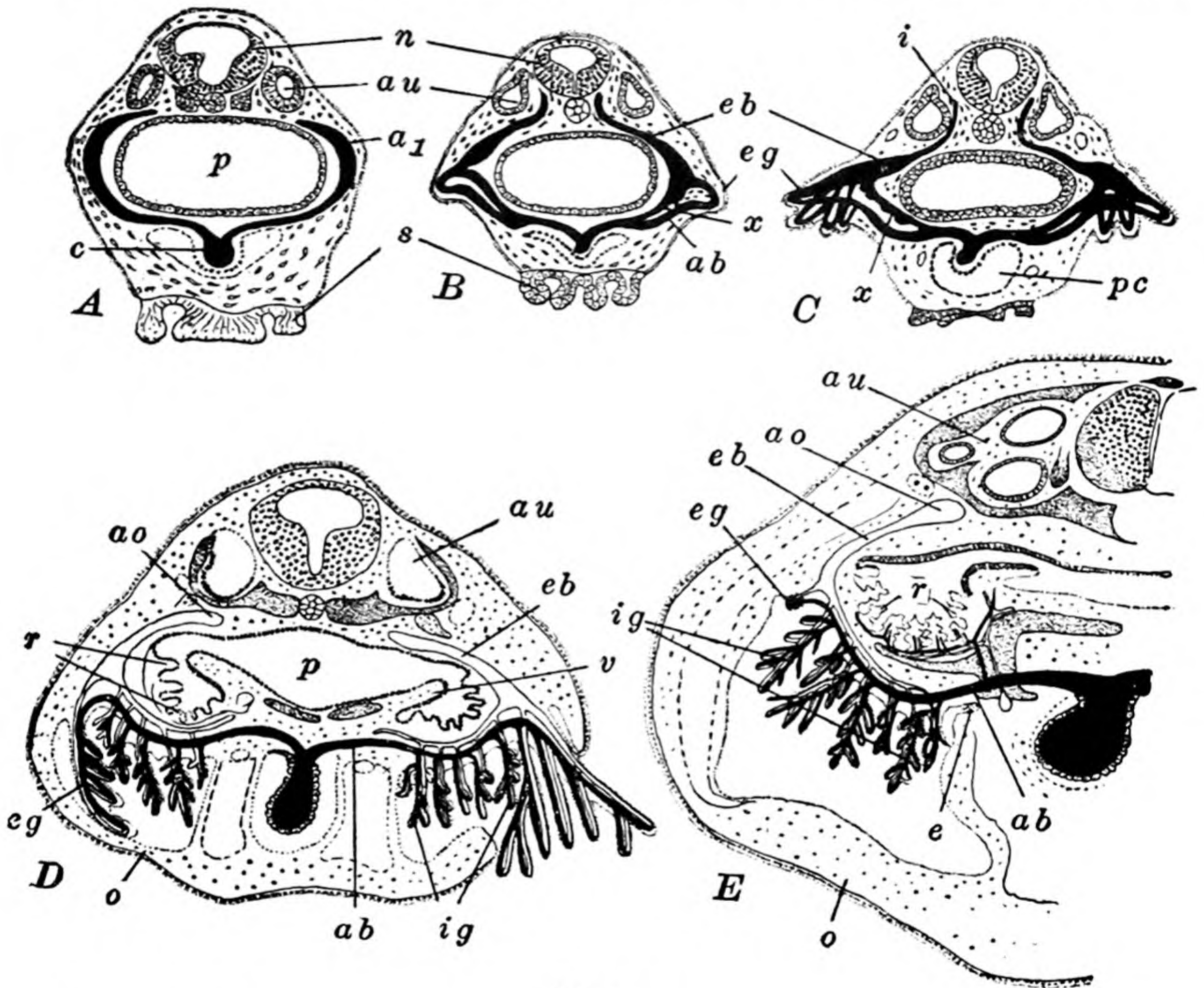
FIG. 541.

Sections through branchial region of tadpoles of *Rana esculenta*, showing development of gills and history of aortic arches (after Maurer, from W. E. Kellicott, *Chordate Develt.*, 1913). A, 4 mm. larva showing continuous first branchial aortic arch. B, 5 mm. larva showing anastomosis between the afferent and efferent portions of aortic arch. C, 6 mm. larva with vascular loops in external gills. D, 13 mm. larva. On the left opercular cavity is closed and external gill is beginning to atrophy, while on the right this cavity is still open and external gill well developed and projecting through opercular opening. E, 17 mm. larva, vessels of second branchial arch; external gill represented only by a minute pigmented vestige. *a* 1, First branchial aortic arch; *ab*, afferent branchial artery; *ao*, root of lateral dorsal aorta; *au*, auditory organ; *c*, conus arteriosus; *e*, epitheloid body; *eb*, efferent branchial artery; *eg*, external gill; *i*, internal (anterior) carotid artery; *ig*, internal gills; *n*, nerve cord; *o*, operculum; *p*, pharynx; *pc*, pericardial cavity; *r*, gill-rakers; *s*, oral sucker; *v*, velar plate; *x*, anastomosis between afferent and efferent branchial arteries.

region. Already in the Amphibia these changes have begun, but it is not till the Amniote grade of structure is reached that they are fully carried out.

Concerning the general development it may be mentioned that the paired rudiments of the dorsal aorta fuse to a median vessel posteriorly, but remain separate in the branchial region and lead to the internal

carotid arteries.[1] The ventral aorta divides anteriorly into paired branches, giving rise to the external carotids, represented in Anura by the lingual arteries. The usual six pairs of lateral aortic arches are laid down in early stages ; and it should be noticed that the so-called aortic arches of adult Tetrapods do not strictly correspond to them alone, but may include a portion of the original ventral aorta below and of the lateral dorsal aorta above.

The early development of the blood-vessels in the Anuran tadpole is much specialised and differs considerably in different forms (Goette, 1875 ; Marshall and Bles, 846 ; Boas, 813 ; Maurer, 849) ; but the general results obtained chiefly by Marshall and Bles may be summarised as follows. The first or mandibular aortic arch persists but little as the ' pharyngeal ' artery. The second or hyoidean disappears. The third
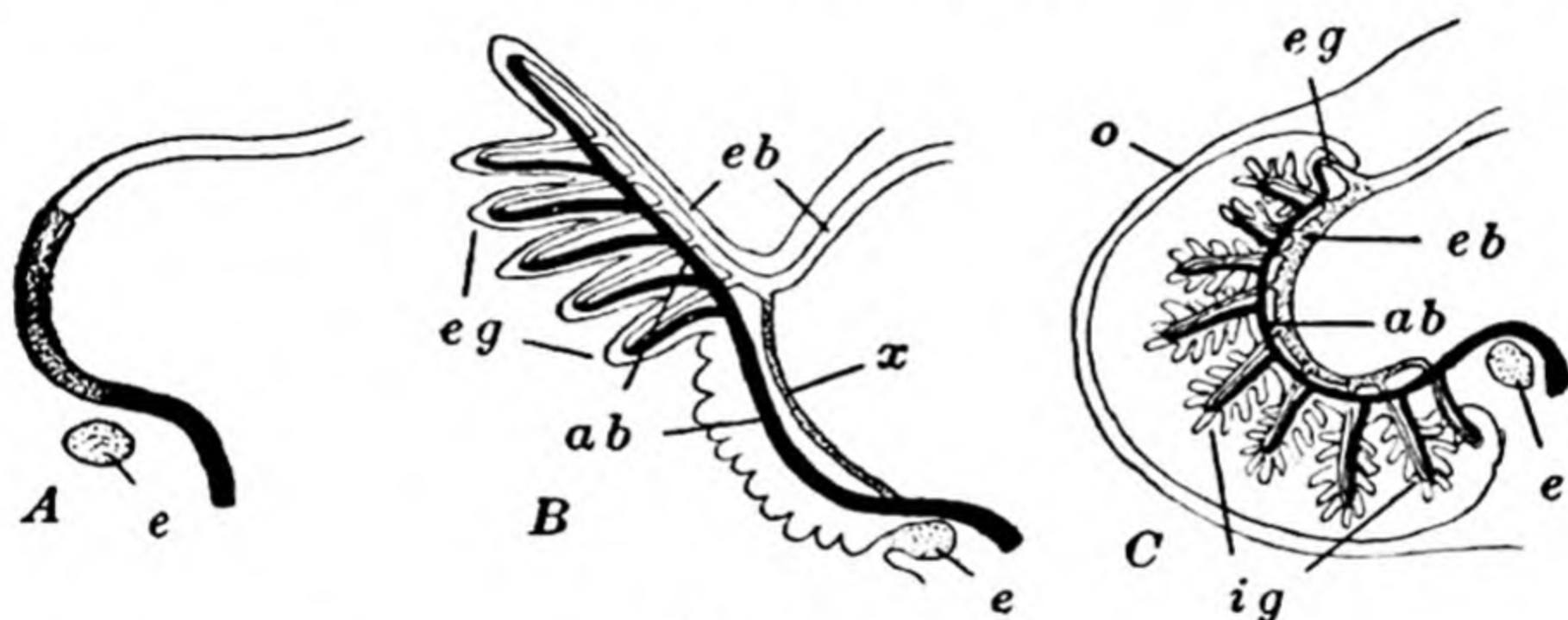
FIG. 542.

Diagrams of aortic arch of adult frog and tadpole (after Maurer, from W. E. Kellicott, *Chordate Develt.*, 1913). A, Continuous aortic arch of adult, showing parts corresponding with larval vessels. B, First external gill and associated vessels in young tadpole. C, Internal gill and associated vessels in tadpole after disappearance of external gills. *ab*, Afferent branchial artery ; *e*, epithelioid body ; *eb*, efferent branchial artery ; *eg*, external gill ; *ig*, internal gill ; *o*, operculum ; *x*, direct anastomosis between afferent and efferent branchial arteries.

aortic arch remains as the so-called carotid arch, carrying arterial blood from the truncus arteriosus to the external and internal carotid arteries. The fourth aortic arch remains as the chief or systemic arch which joins its fellow to form the dorsal aorta. The fifth arch disappears, and the sixth gives rise to the pulmo-cutaneous arch taking chiefly venous blood to the skin by its cutaneous branch and the lung by its pulmonary artery, Fig. 540.

Important specialisations characteristic of Tetrapods generally have appeared. The task of carrying the forward stream of blood to the head is now assumed by the third aortic arch, and that part of the lateral dorsal aorta between the third and fourth arches, known as the ductus caroticus, is atrophied. Since, however, the ductus caroticus still persists

[1] The bifurcation of the aorta tends to be carried farther backwards in later stages owing to the secondary splitting of the median aorta in Tetrapods generally.

in Apoda, in some adult Urodela, such as *Triton* (Boas, **813**), and some adult Reptilia (*Sphenodon, Alligator* (?)), and many Lacertilia (Rathke, 1843, 1857; van Bemmelen, **809**; Beddard, 1904-6; O'Donoghue, **852**), its obliteration has probably taken place independently in Amphibia and Amniota. The same may be said of the ductus Botalli (ductus arteriosus), that dorsal part of the sixth aortic arch which joins the pulmonary artery to the dorsal aorta. Closed and reduced to a fibrous strand in adult Anura and the majority of Amniotes, it survives as an open vessel in Apoda, Urodela, *Sphenodon, Alligator,* and some Chelonia. *Sphenodon,* indeed, is the only Amniote normally preserving both these ducts in the fully developed adult.

The fifth aortic arch disappears entirely in all adult Tetrapods except the Urodela. It is always small even in the embryo, and vanishes so quickly that for a long time it was unidentified in Amniotes until van Bemmelen (1886) described it in the embryo of Reptiles and Birds, and Zimmermann (1888) in that of Man and other Mammals, Figs. 543-4, 548.
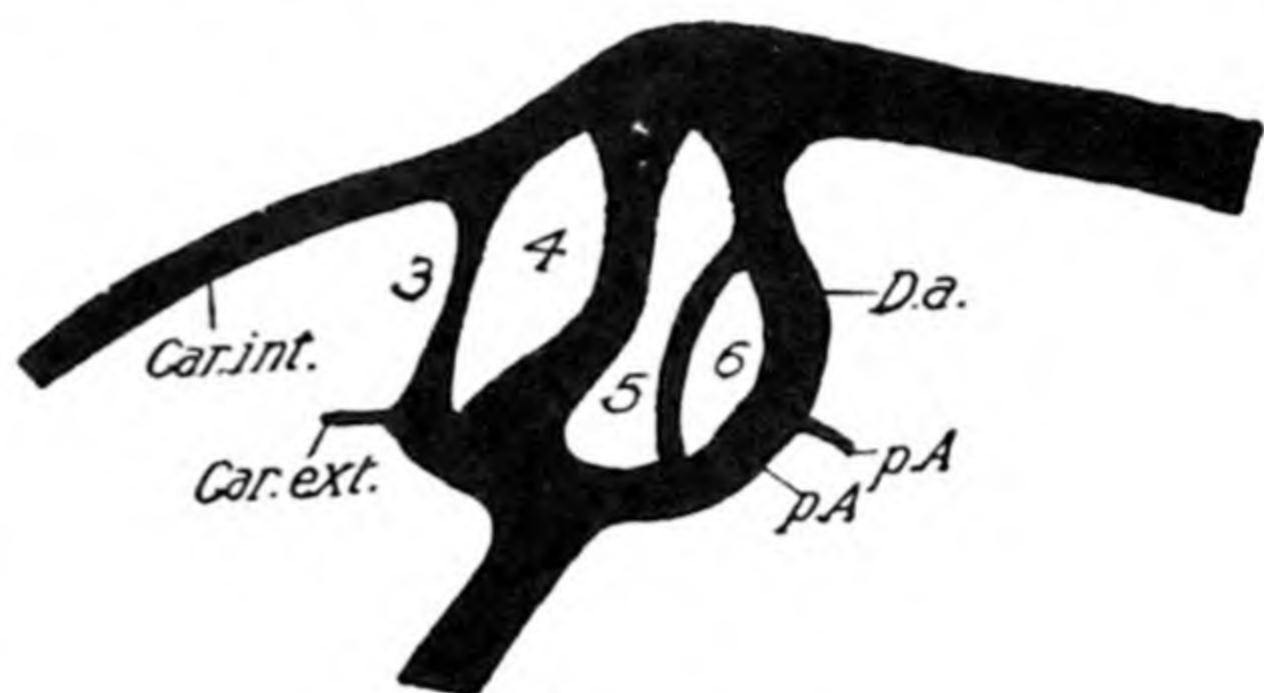
FIG. 543.

Aortic arches of left side of chick embryo, 4½ days old. From an injected specimen. (After Locy, from F. R. Lillie, *Devel. Chick*, 1919.) *Car.ext*, External carotid; *Car.int*, internal carotid; *D.a*, ductus arteriosus; *p.A*, pulmonary artery; 3, 4, 5, 6, third, fourth, fifth, and sixth aortic arches.

The ventral aorta always becomes spirally split to its base, being thus divided into a pulmonary trunk leading venous blood to the pulmonary arteries, and an aortic trunk leading to the systemic and carotid arches ; for these two pairs of arches are always associated.

It is a familiar fact that in the Mammalia a complete aortic arch persists on the left side only. At an earlier stage in ontogeny the fourth aortic arches were complete on both sides, each giving off a subclavian artery ; but later the arch on the right atrophies posteriorly to the origin of the subclavian. What remains of the arch as far as its junction with the common carotid is now called the subclavian artery, and the region of the lateral ventral aorta leading to them is called the innominate artery.

The specialisation of the aortic system in the modern Reptilia and Birds has proceeded on different lines from the Mammalian and must apparently have started before the obliteration of the ductus caroticus and ductus Botalli. In these groups not only has the pulmonary trunk been separated off from the original ventral aorta, but the remaining aortic trunk has also been spirally split to its base, so that two aortic trunks are formed.

The smaller left arch now comes from the right side of the heart, and the larger right from the left side of the heart. In Birds only the latter persists (see, further, p. 562). An important point to notice is that in all living Reptiles and in Birds the base of the carotid trunk, formed by the union of the right and left carotid arches (third aortic arches), opens into the
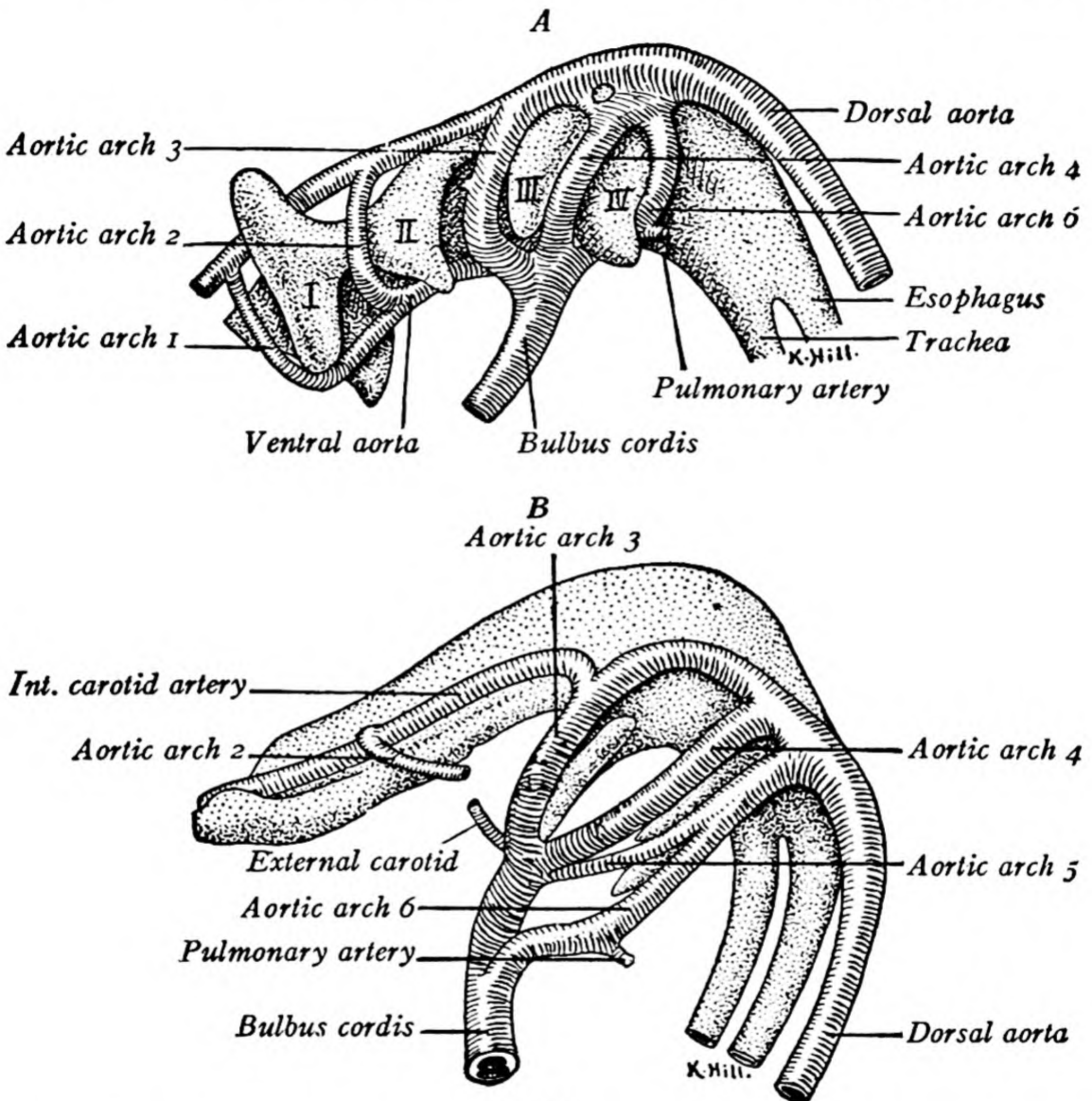

FIG. 544.

Aortic arches of human embryos : A, 5 mm. ; B, 7 mm. (after Tandler). *I-IV*, Pharyngeal pouches. (From Prentiss and Arey, *Text-book of Embryology*, 1917.)

larger right aortic trunk, and the whole aortic arch system is characteristically a s y m m e t r i c a l in a manner differing radically from the asymmetry of the mammalian system. The significance of this divergence will be discussed later (p. 572).

As the neck becomes lengthened the vessels of the carotid system become correspondingly elongated, Figs. 545-6. In Mammals all the arches **retreat** backwards with the heart and the internal and external carotids

are lengthened ; and the same thing happens in short-necked Lacertilia, Chelonia, Crocodilia, and Aves. In the two last groups the external and internal carotids anastomose anteriorly, and if the latter fuse to a median vessel the right carotid arch may then atrophy (Crocodilia). In Birds the external carotids usually atrophy ; the internal carotids may fuse, and then the base of either the left or the right atrophy. Another
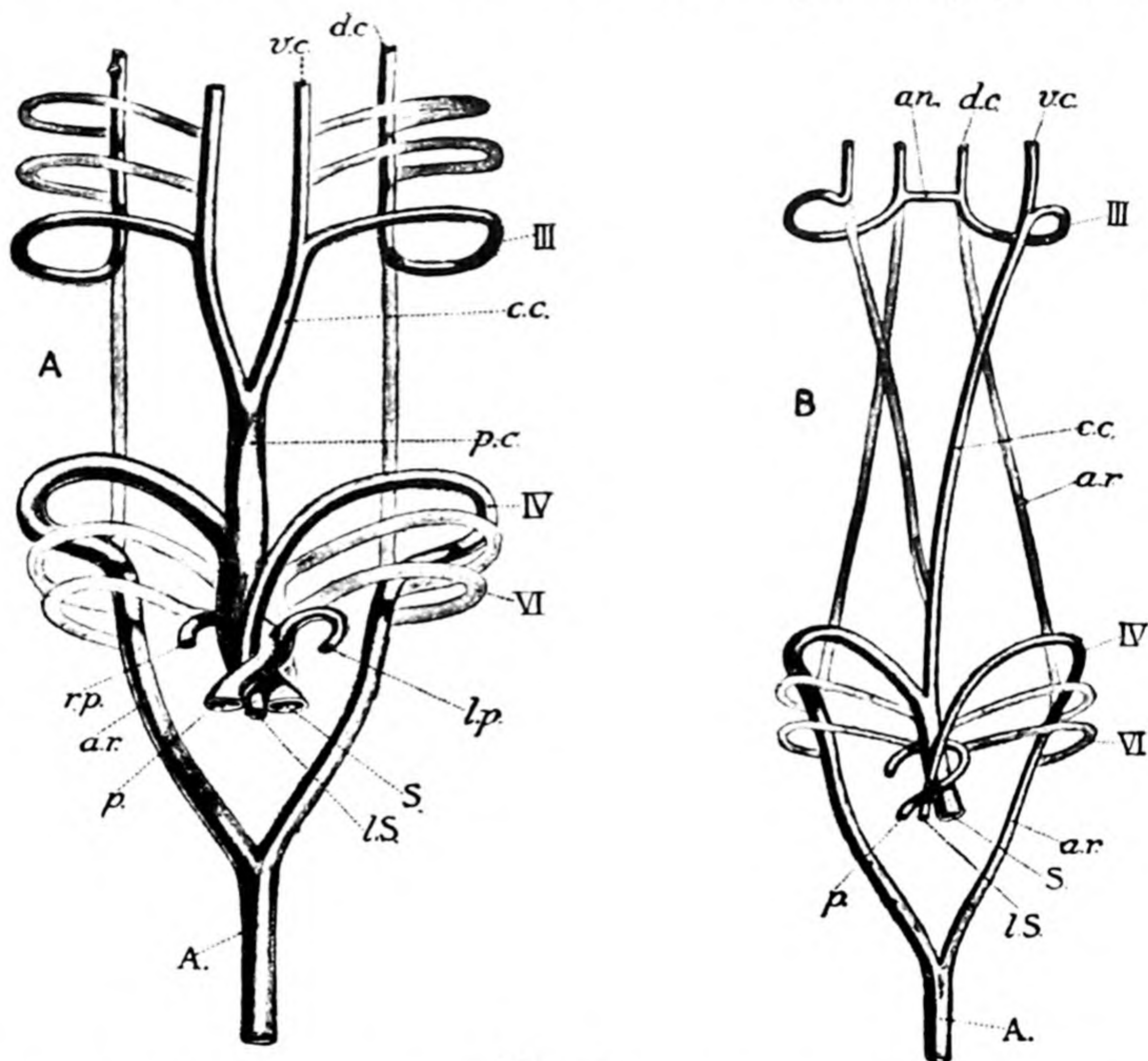
FIG. 545.

Illustrating modification of the carotid arteries, correlated with elongation of the neck region. A, Varanid lizard ; B, grass-snake (*Tropidonotus*). *p.c*, Primary carotid ; *A*, dorsal aorta ; *a.r*, aortic root ; *an*, anastomotic vessel ; *c.c*, common carotid ; *d.c*, dorsal (internal) carotid ; *l.p*, left pulmonary artery ; *l.s*, left systemic ; *p*, pulmonary ; *r.p*, right pulmonary ; *S*, systemic aorta ; *v.a*, ventral aorta ; *v.c*, ventral (external) carotid ; III, IV, VI, aortic arches.

modification takes place in certain Lacertilia (Varanidae) and in the Ophidia ; here the carotid arches remain near the head and so become widely separated from the systemic arches, Figs. 545-6.

Before entering the cranial cavity the internal carotid gives off a palatine branch which runs forwards below the basis cranii. This artery, absent in Elasmobranchs and rarely represented in Teleostomes, occurs in the Dipnoi. After having entered the cranial cavity the internal carotids provide as usual cerebral arteries and a basilar artery to the central nervous system, small arteries to the pituitary body, and an

'ophthalmic' artery on each side, which issues with the optic nerve and no doubt corresponds to the optic and ophthalmic artery of the fish.
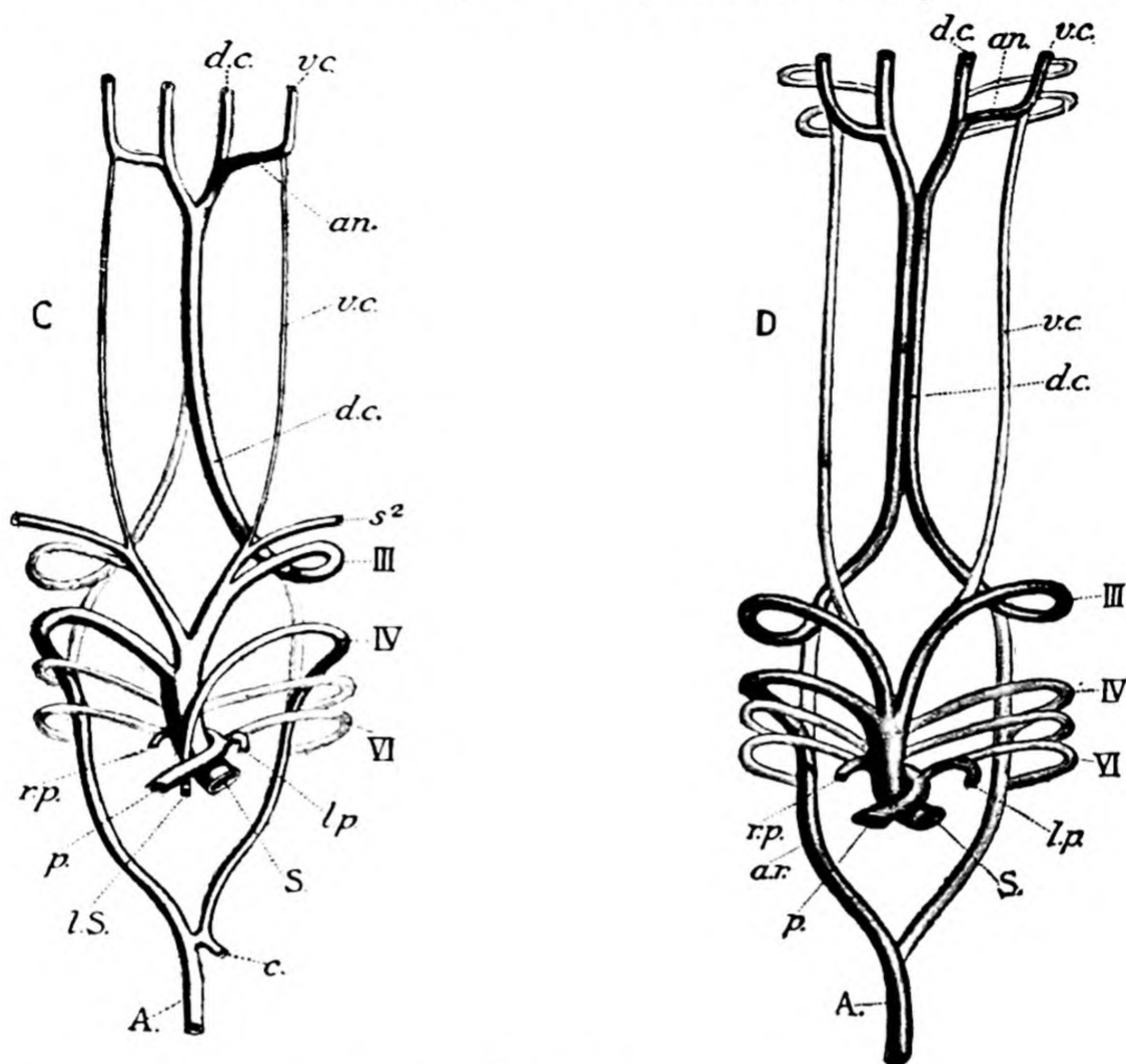
FIG. 546.

Illustrating modification of the carotid arteries, correlated with elongation of the neck region. C, Crocodile; D, bird. c, Coeliac artery; s², secondary subclavian. (Other letters as in Fig. 545.)

BRANCHES OF THE INTERNAL CAROTIDS : OPHTHALMIC AND STAPEDIAL ARTERIES

From the description given above of the arterial system of the head region, it appears that the specialisation of the cephalic arteries has had a considerable influence on the fate of the aortic arches and on the differentiation of the heart in the Vertebrate series. There remains to be discussed the homology of certain arteries and their relation to the skeletal and surrounding parts (Allis, 802-6; de Beer, 421).

The fundamental relations of the internal carotids have already been described (p. 272). Each internal carotid is a prolongation of the lateral dorsal aorta, and gives off after entering the cranial cavity not only cerebral arteries but also an optic artery (so-called ophthalmic of Tetrapods), which passes out to the retina of the eye with the optic nerve. In

Pisces it also gives off a more posterior ophthalmic artery to the chorioid plexus of the eye, Figs. 247, 288. Both these arteries issue from the skull in front of the pila antotica, and dorsally to the trabecula cranii. On the other hand the aortic arches join the lateral dorsal aorta ventrally to the basis cranii. The Elasmobranchs are the only exception to this rule (p. 517), for in them the mandibular aortic arch (efferent pseudobranchial) joining the ophthalmic outside passes into the cranial cavity through a foramen dorsally to the trabecula, Figs. 246, 247. This condition is probably due either to a difference in the assemblage of the cartilages of the posterior trabecular region (Allis, 670), or more probably to a loss of the original connexion of the mandibular arch with the carotid after its junction with the dorsally placed ophthalmic artery (de Beer, 421). No evidence of such a ventral connexion has, however, been found in the embryo of Selachians. In Teleostei these vessels are typically related in early stages, but, owing to the interruption of the original connexion with the lateral dorsal aorta of the efferent pseudobranchial, the latter passes intracranially directly into the ophthalmic artery in the adult, and this artery issues of course dorsally to the trabecula, Figs. 284, 288-9, 537-8 (see p. 518). The apparently abnormal relation of the internal carotid to the trabecula in Mammalia is discussed elsewhere (p. 263).

Of great significance in determining the homologies of the stapes and parts of the ' middle ear ' in Tetrapods is the stapedial artery (p. 467). This artery can be traced with considerable certainty from Man down to the lowest fishes, where it appears to be represented by the orbital artery, the so-called external carotid of many authors (Allis, 802-6; Schmalhausen, 699; Versluys, 769-70; Goodrich, 734; de Beer, 421). In Gnatho-stomes generally an artery is found branching off from the dorsal end of the second or hyoidean aortic arch or from the lateral dorsal aorta in front of that arch, Fig. 547. Its primary morphological relations are as follows : it is dorsal and posterior to the first (spiracular) gill-pouch, ventral to the hyomandibula in fishes ; it passes forwards through the cranio-quadrate passage to the orbit, below the otic process of the quadrate (p. 412) ; its branches pass outwards above the palatoquadrate bar and behind the processus ascendens to supply the side of the head and jaws. There are three main branches : the supraorbital, infra-orbital to upper jaw, and mandibular to lower jaw (Tandler, 875-7 ; Grosser and Brezina, 832 ; Shiino, 870 ; O'Donoghue, 852 ; Twining, 878 ; Hafferl, 833-4). In Selachians the orbital artery may, owing to the outward growth of the subocular shelf, come to pierce the cartilage on its way to the orbit, and become partially buried in the wall of the auditory capsule. In *Amia* it is enclosed in the jugular canal, while in

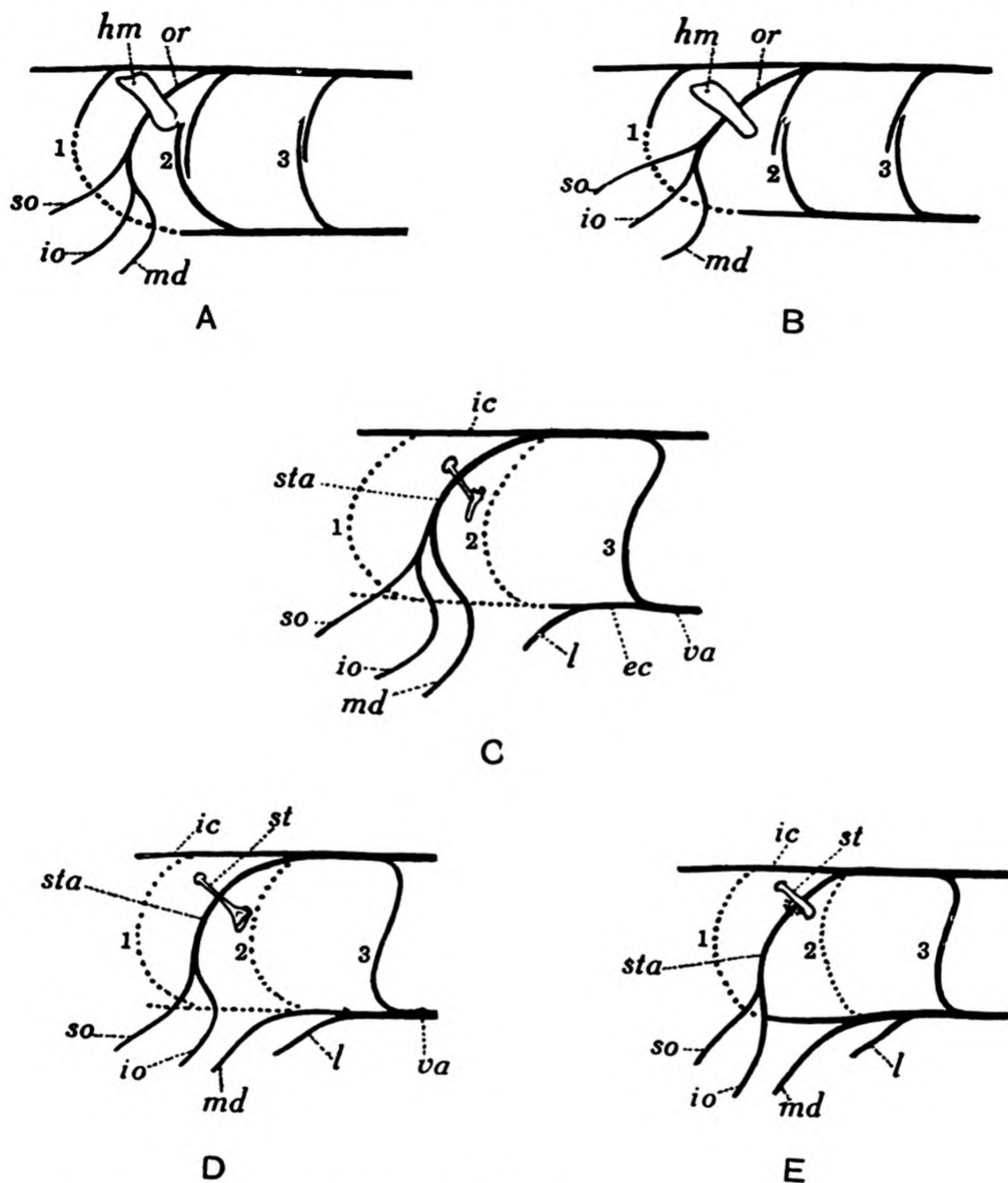*Lepidosteus* and most Teleosts it appears to be represented by two vessels,

FIG. 547.

Diagrams illustrating fate of first three Aortic Arches, 1, 2, 3, and relation of Orbital or Stapedial Artery to Hyomandibula in : A, Selachian ; B, Teleostome ; C, Lacertilian ; D, Crocodilian ; E, Monotreme. Left-side views. *ec*, External carotid ; *hm*, hyomandibula ; *ic*, internal carotid ; *io*, infraorbital ; *l*, lingual ; *md*, mandibular ; *or*, orbital ; *so*, supraorbital ; *st*, stapes or columella auris ; *sta*, stapedial artery ; *va*, ventral aorta.

one passing through the jugular canal and the other through the subocular shelf farther forward, Fig. 284.

The orbital artery is typically developed in Dipnoi (*Ceratodus*) and in Tetrapods, where it is known as the stapedial artery and often pierces

the stapes (p. 467). It has essentially the same relations and distribution as in Selachians, but complications arise owing to anastomosis with the ventral true external carotid, which tends to rob it of some or all of its branches. This external carotid is an extension of the ventral aorta supplying thyroid, lingual, and sometimes mandibular branches. Even
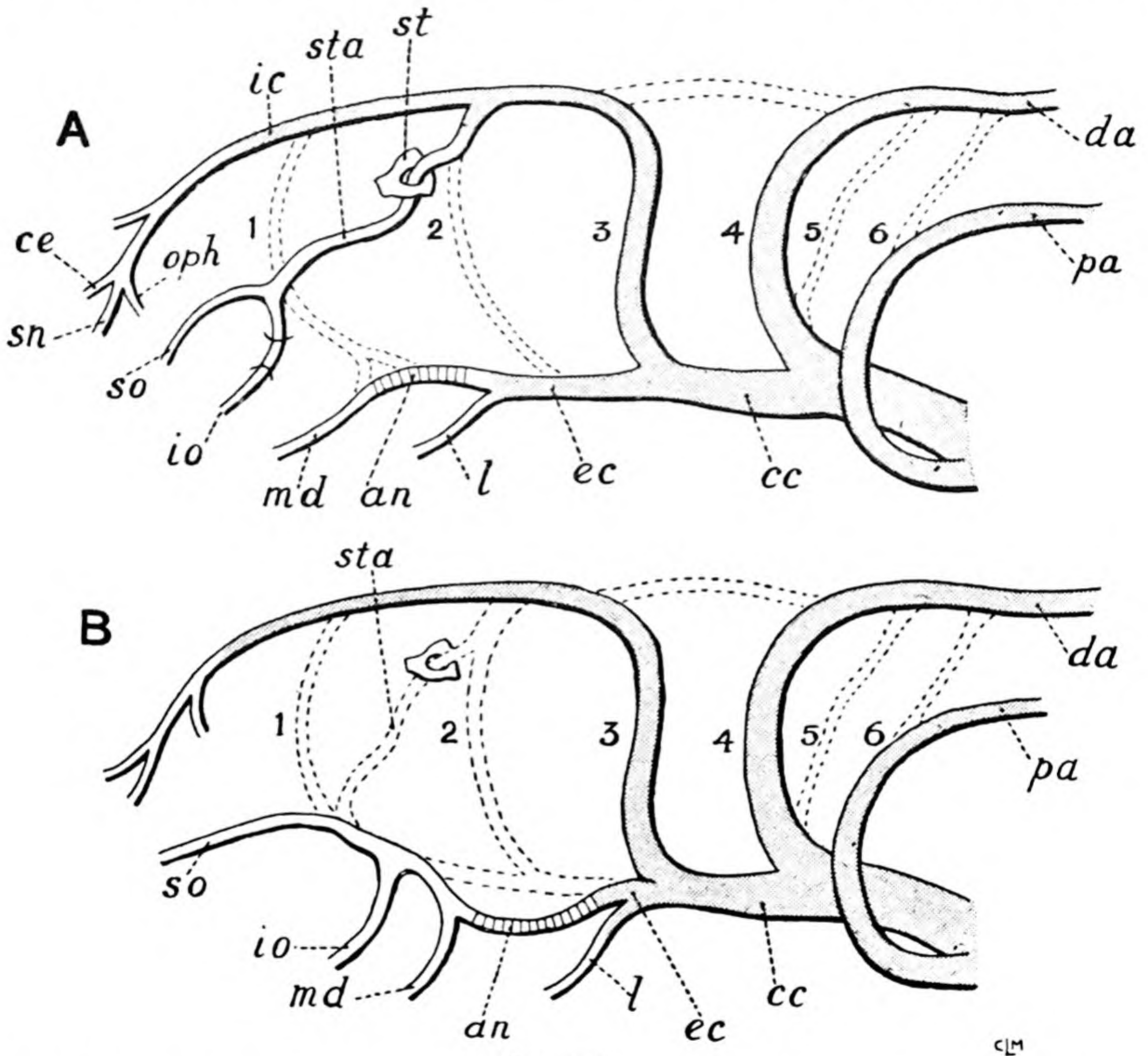
FIG. 548.

Diagram of left-side view of arterial arches and cephalic arteries in Rat, A, and Man, B (partly from J. Tandler). *an*, Secondary anastomosis ; *cc*, base of carotid arch ; *ce*, cerebral artery ; *da*, dorsal aorta ; *ec*, external carotid ; *io*, infraorbital ; *l*, lingual ; *md*, mandibular ; *oph*, ophthalmic ; *pa*, pulmonary ; *so*, supraorbital ; *st*, stapes ; *sta*, stapedial artery. 1-6, Six embryonic aortic arches.

in Reptilia it tends to join the mandibular branch of the stapedial (Crocodile) ; and in Mammalia, although the stapedial artery is developed in the embryo with its three main branches, in later stages an anastomosis is established with one or more of these, and their original connexion with the dorsal aorta through the stapedial artery is lost (Tandler, 876). Thus in the rat the stapedial artery persists in the adult, Fig. 498, but gives off only the supra- and infraorbital branches, while in Man

and most Ditrematous Mammals all three branches join the external carotid and the stem of the stapedial is lost, Fig. 548. The morphological significance of the stapedial artery is further discussed above (p. 472).

THE CHIEF VEINS OF THE HEAD

The veins of the head region are of considerable importance not only as forming part of the vascular system, but also for the elucidation of the homologies of the skeletal elements. For in spite of many modifications in the Vertebrate series the veins on the whole preserve very constant relations to the surrounding structures.

The venous blood from the anterior region in Gnathostomes returns to the heart by a system of veins derived from or connected with the anterior cardinals (p. 508).[1]

On each side cerebral veins issuing from the cranial cavity and orbital veins join to a jugular vein, which, receiving a ventral external jugular and a subclavian vein from the pectoral region, passes back into the ductus Cuvieri (vena cava anterior or precaval vein of higher forms). In Mammals a ventral cross connexion often develops between the two precavals, and the left precaval may then be interrupted and the blood flow into the right as in Man and other Placentals (in Insectivora, Cheiroptera, Ungulata, and many Rodentia, however, both precavals persist even when a commissure is formed).

From the point of view of the general morphology of the head, the chief interest centres round the development of the jugular vein and its main branches in Craniates (Hochstetter, 835; Salzer, 866; Grosser and Brezina, 832; van Gelderen, 824). In early stages the embryonic anterior cardinal veins run forwards on either side of the notochord below and medial to the roots of the spinal nerves and the myomeres. They are continued forwards over the gill-pouches and medial to the cranial nerves and auditory sac as the venae capitis mediales draining blood from the brain. Just behind the developing hypophysis they become united by a transverse hypophysial vein passing ventrally to the original tip of the notochord, Figs. 242, 245, 256.

The tributaries of the longitudinal v. capitis medialis become differentiated into an anterior cerebral vein (from the eye and fore-brain), a middle cerebral vein (from the middle region of the brain including the cerebellum), and a posterior cerebral vein (from the remainder of the

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[1] In Cyclostomata these veins, although built on the same general plan, undergo some peculiar modifications mentioned in connexion with the heart, p. 543.

hind-brain). The v. cap. medialis receives the last vein behind the auditory sac near the vagus nerve, the middle vein near the root of the facial nerve in front of the auditory sac, and reaches forwards to the anterior vein. This system of embryonic head veins is situated within the cranial cavity; but the v. capitis medialis soon becomes more or less completely replaced by another more lateral longitudinal vein, the vena capitis lateralis, which develops outside the cranial
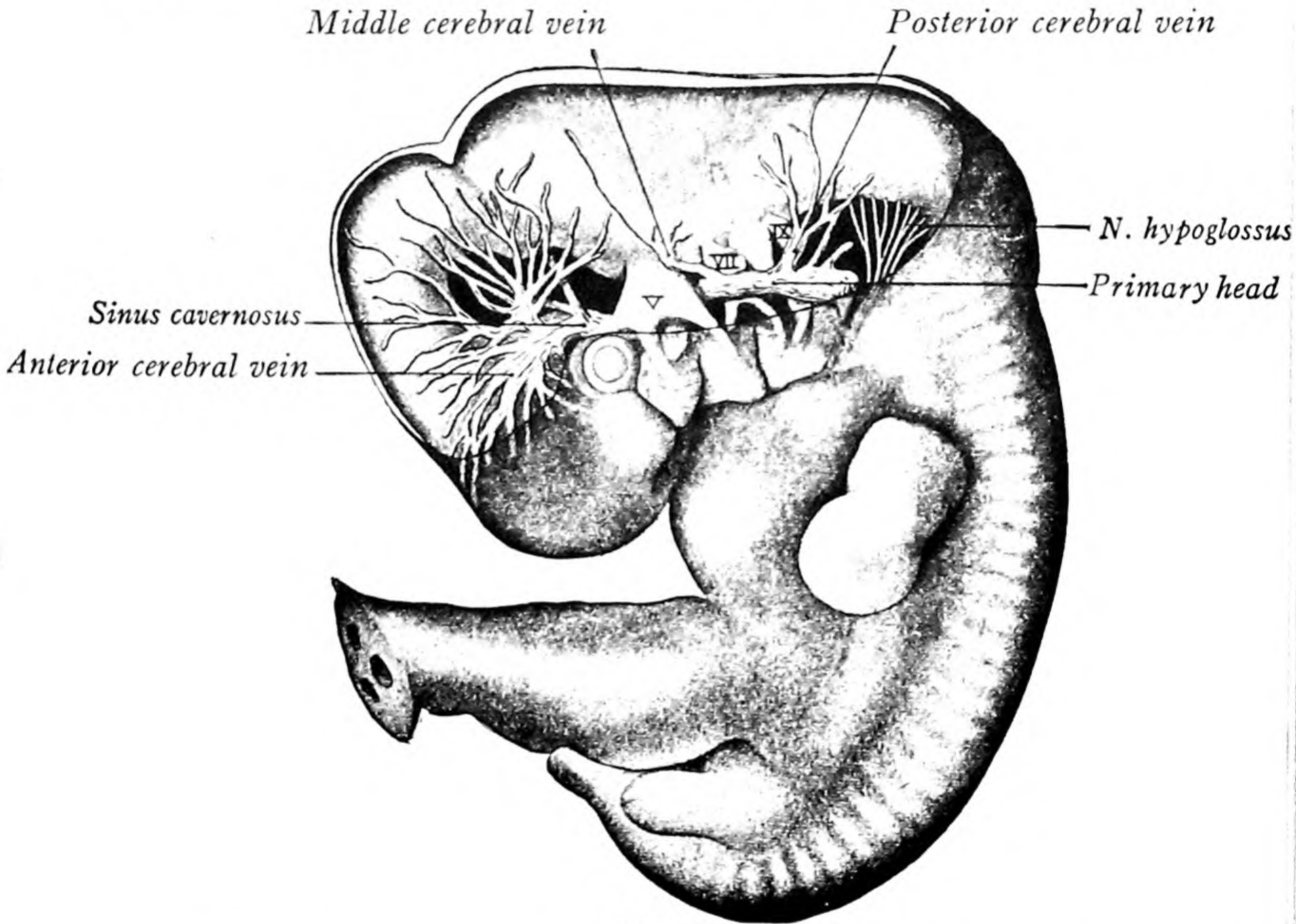
FIG. 549.

Veins of head of 9 mm. human embryo (after Mall.) × 9. (From Prentiss and Avey, *Text-book of Embryology*, 1917.)

wall and flows into the anterior cardinal behind the vagus nerve. The v. cap. lateralis arises from a number of loops which grow round the auditory sac and cranial nerves from the v. cap. medialis, and fuse to a longitudinal vessel outside them. As this v. cap. lateralis becomes completed the inner vein tends to disappear, remaining only in so far as is necessary to enable the tributaries to communicate with the outer one. Thus the v. cap. medialis always disappears in the region of the auditory sac, but remains on the inner side of the trigeminal nerve to receive the anterior cerebral, ophthalmic, and hypophysial veins, and passes out through the wall of the skull with the facial nerve to join

the v. cap. lateralis.　　The posterior cerebral vein flows into the v. cap. lateralis farther back, passing out of the skull with the vagus nerve through the jugular foramen, Figs. 245-6, 550.

FIG. 550.—Diagrams of *veins of head* in Gnathostomes ; left-side view with optic and auditory capsules and trigeminal nerve in outline (from C. van Gelderen, *Z. f. Anat. u. Entwickl.*, 1925).

The adult jugular vein (head vein, Stammvene) is, then, of mixed origin, and varies considerably in composition in different groups. Throughout all the Gnathostomes, however, its development is similar, and the transverse hypophysial vein passes out of the skull just anteriorly to the pila antotica (p. 244).

That part of the jugular vein derived from the v. cap. lateralis persists in Cyclostomata, Pisces, Amphibia, Reptilia,[1] Monotremata, and Marsupialia. It runs outside the auditory capsule backwards alongside the hyomandibular branch of the facial nerve through the cranio-quadrate passage (p. 412) and dorsally to the spiracular gill-pouch. In Selachians it runs dorsally to the hyomandibular cartilage (p. 416), and in the Tetrapods dorsally to the columella auris or stapes (p. 467). In Teleostomes it runs through a short jugular canal in the thickness of the wall of the auditory capsule (p. 276), and passes medially and ventrally to the hyomandibula, being apparently represented in this region by two veins, Fig. 446. A third venous loop occurs in some Teleostei passing outside the hyomandibular (de Beer, 421). Occasionally (as in Cyclostomata, most Selachii, Polypterini, and Anura) the v. cap. lateralis continues forward to the orbit outside the trigeminal nerve. But usually this nerve passes laterally to the head vein, which is then derived here from the v. c. medialis.

Among the Tetrapods there is a progressive tendency for the blood from the brain to drain into a newly formed median dorsal sinus passing backwards to the posterior cerebral veins. The connexion of the anterior cerebral vein with the v. cap. medialis is lost ; but the middle cerebral vein persists, except in the higher Mammalia, issuing into the orbit with the facial nerve. In the Lacertilia (except Amphisbaenidae) the original connexion of the posterior cerebral vein with the jugular is lost, and the blood is carried out behind the occipital arch ; in Chelonia, however, both outflows are present (Grosser and Brezina, 832 ; Versluys, 769 ; Bruner, 817).

While the v. cap. lateralis still persists in Monotremes and Marsupials, it disappears for the most part in adult Placental Mammalia. Anastomoses occur and it is replaced by intracranial sinuses which carry the blood back to the posterior cerebral vein and so out by the jugular foramen to the ' internal jugular vein '.

From the brief account given above it appears that the vena capitis medialis and the vena capitis lateralis are constantly developed in the embryo of all Craniata, and that they and their branches bear important relations to the skeletal and other parts. They always contribute to the formation of the adult jugular vein. The external jugular vein, another branch from the ductus Cuvieri, is more variable in extent, seems to develop independently, and drains usually the more ventral and lateral regions of the head, including sometimes the lower jaw.

[1] In Crocodilia and Aves it is replaced by a secondary outer vein (van Gelderen).

THE HEART

The heart of the Craniate Vertebrates is a specialised part of the primary longitudinal ventral vessel, and is a muscular pumping organ adapted in the first place to drive the venous blood forward and upward through the gills. Consequently it develops just behind the gills and in front of that point where the ventral vessel receives the venous blood from the body-wall and the alimentary canal by the ductus Cuvieri and hepatic veins (see p. 506).

The Acrania (Cephalochorda) represent an earlier stage in the phylogeny of Vertebrates before the differentiation of a heart, since in them the subintestinal vein (somewhat broken up on the liver) is continued forwards into the pharyngeal region as a ventral aorta without special enlargement. The venous blood in *Amphioxus* is propelled along this ventral aorta, which has contractile muscular walls, and up the branchial vessels of the primary gill-bars with the help of bulbous enlargements at their base. The ventral aorta is suspended in the coelom below the endostyle, and the main branchial vessel passes up the bar on the inner side of its coelomic canal,[1] Fig. 707.

The relations of the vessels and cavities in Craniates are fundamentally similar (p. 490), but the coelomic cavities of the bars are early suppressed, and the ventral coelomic cavity is concentrated as it were round the heart to form the pericardial coelom. The latter cavity is of course at first paired, the right and left cavities being separated by a primary longitudinal mesentery, and it is between the two folds of this mesentery (mesocardium) that the heart is developed. Very soon the ventral mesocardium disappears leaving at most some connecting strands, and later the dorsal mesocardium also breaks down except at the anterior and posterior ends where the cardiac tube pierces the wall of the pericardial coelom. Except at its two ends the heart now lies freely in the protective pericardial cavity, and is thus enabled to become coiled, to enlarge, and to pulsate. The early development of the heart is so well described in current text-books that only a few points need here be mentioned, Fig. 551.

In ontogeny as in phylogeny the heart first appears as a longitudinal

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[1] From the afferent vessels three branches pass up each primary bar and join again to open into the dorsal aorta. A loop of two vessels extends down to near the ventral end of the secondary bar, receiving blood from the primary bar through the cross-bars or synapticula, and also opens into the dorsal aorta. Dorsally the efferent vessels on each side are joined by a longitudinal commissural vessel which breaks up at intervals into a capillary network supplying the nephridia (Spengel, Benham, Boveri, **814**).

median vessel : Cyclostomata, Elasmobranchii, Teleostomi (except Teleostei), and Amphibia. But in Teleostei and Amniota, where the embryo develops as a flattened blastoderm overlying a yolk-sac, and where the closure and separation of the alimentary canal is delayed, the heart
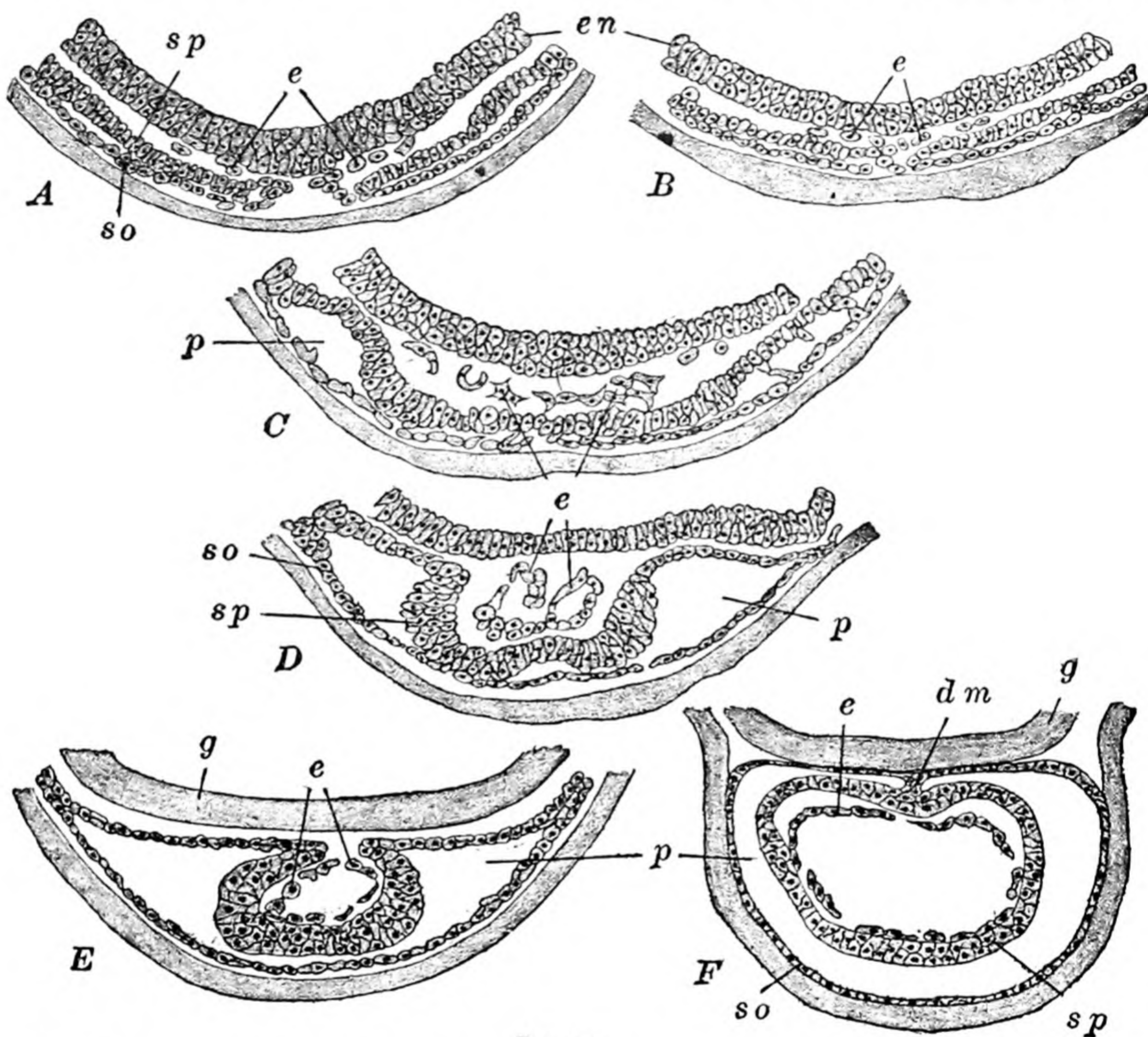
FIG. 551.

Sections showing formation of heart in frog. A-D, Series of transverse sections through corresponding regions of a series of embryos of *R. temporaria* ; E, F, sections through same region in older embryos of *R. sylvatica*. (After Brachet, from W. E. Kellicott, *Chordate Develt.*, 1913.) A, 2·6 mm. embryo, mesoderm approaching mid-line ; endothelium appearing. B,(Older embryo of same length as A. C, 3 mm. embryo showing enlargement of pericardial cavity and beginning of folding of somatic mesoderm. D, 3·2 mm. embryo, endothelial cells becoming arranged in form of a tube. E, Embryo of about 3 mm. F, Embryo of 5-6 mm. Heart tube established ; dorsal mesocardium still present. *dm*, Dorsal mesocardium ; *e*, cardiac endothelial cells ; *en*, endoderm ; *g*, wall of gut (pharynx) ; *p*, pericardial cavity ; *so*, somatic layer of mesoderm ; *sp*, splanchnic layer of mesoderm.

develops from paired rudiments which fuse in the middle line below the fore-gut at a later stage. The outer wall of the tubular heart is formed by the enveloping splanchnic mesoblast or visceral layer of the pericardium, and becomes the thin adult ' epicardium '. The thin inner lining is formed of a special endothelium, yielding the ' endocardium ' of the adult. It is derived from cells which gather between the splanchno-

pleure and the yolk-cells, and are in all probability of mesoblastic origin. The thick muscular layer between the endocardium and epicardium, and known as the 'myocardium', is developed from mesenchymatous cells proliferated from the medial surface of the splanchnopleure, Fig. 551.

The originally straight cylindrical cardiac tube becomes differentiated into four primary regions or chambers separated by constrictions—a posterior sinus venosus, atrium, ventricle, and anterior bulbus cordis,[1] Fig. 552. The sinus venosus bulges into the pericardium from its posterior wall, and receives all the venous blood from the hepatic veins and right and left ductus Cuvieri, which open freely into it ; also from the heart itself by the cardiac vein. The sinus opens into the atrium in front by an aperture guarded by two sagittal sinu-auricular valves. The atrium communicates with the ventricle by an atrio-ventricular aperture also provided with two valves, the region leading to this opening generally forming a narrow (atrial or auricular) canal. The tapering anterior end of the ventricle passes into the bulbus cordis, which is continued into the truncus or base of the ventral aorta outside the pericardial cavity. This bulbus in lower fishes is converted into the conus provided with longitudinal rows of pocket valves—a primitive condition (p. 540). The valves develop from thickenings or folds of the endocardium, are disposed with their concavity in front, and ensure the passage forwards of the blood from chamber to chamber. A backward flow of the blood tends to make them meet and close the lumen, while blood flowing forwards tends to separate them. Whereas the walls of the blood-vessels generally are provided with smooth muscle fibres, the walls of the four chambers of the heart in all Craniates have striated muscle-cells of a peculiar histological structure quite characteristic of this organ. The blood is propelled forwards from chamber to chamber by successive rhythmic waves of contraction starting in the sinus and ending in the bulbus. In the fully developed heart the wall of the sinus is thin, has little muscle, and is only slightly contractile, that of the atrium more muscular and very distensible, while the conus is primitively stiff, muscular, and contractile ;

[1] There has been considerable confusion in the nomenclature of the anterior region of the heart. Bulbus cordis is the name now generally applied by embryologists to the anterior chamber. But the name conus arteriosus, introduced by Gegenbaur to designate the anterior muscular region of the Selachian heart, is often given to it. Moreover, the Selachian conus does not correspond to that part of the heart so called in human anatomy. It is best, then, to apply the name bulbus cordis, introduced by A. Langer, to the embryonic structure throughout the Craniata, and keep the name conus arteriosus for the adult muscular contractile chamber derived from it in Pisces and Amphibia.

but the most effective chamber is the ventricle, whose powerful muscula-ture forms a very thick wall. The lumen of the ventricle is partly invaded
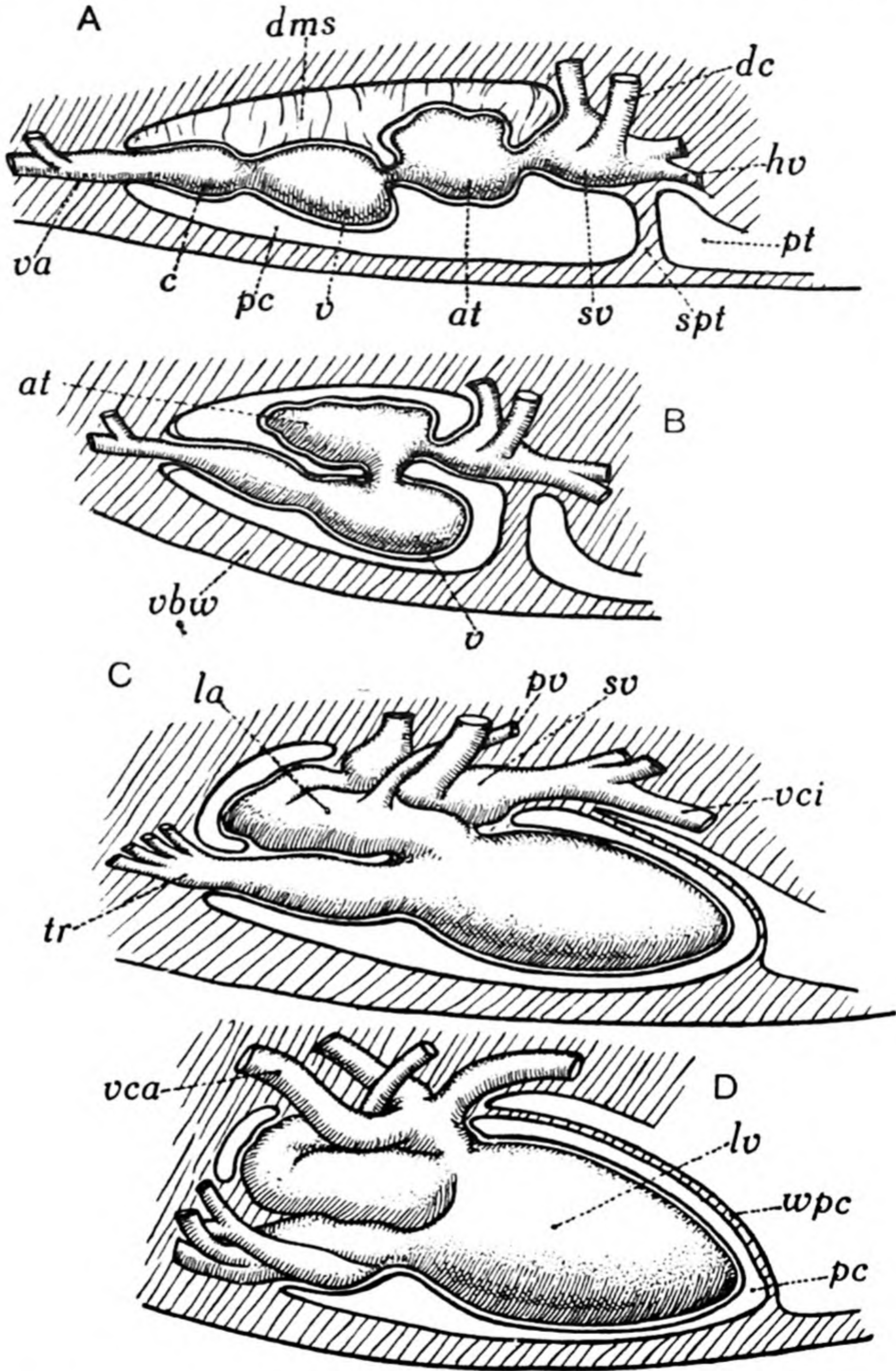
FIG. 552.

Diagrams illustrating the disposition in the pericardial cavity and phylogenetic modification of the chambers of the *heart* in Gnathostomes. A, Hypothetical primitive condition ; B, Selachian stage ; C, Amphibian stage ; D, Amniote stage. *at*, Atrium ; *c*, conus arteriosus ; *dc*, ductus Cuvieri ; *dms*, dorsal mesocardial fold ; *hv*, hepatic vein ; *la*, left auricle ; *lv*, left ventricle ; *pc*, pericardial coelom ; *pt*, peritoneal coelom ; *spt*, septum transversum ; *sv*, sinus venosus ; *tr*, truncus arteriosus ; *v*, ventricle ; *va*, ventral aorta ; *vbw*, ventral body-wall ; *vca*, vena cava anterior ; *vci*, vena cava inferior ; *wpc*, wall of pericardial coelom = *spt*.

and subdivided by muscle strands and trabeculae (columnae carneae) extending inwards, sometimes attached by tendons, and preventing undue

dilatation. Similar but much less pronounced strands may be present in the atrium (musculi pectinati). Tendinous restraining strands (chordae tendineae) may be attached to the edges of the valves, often provided with muscles (musculi papillares) in the higher forms.

The cardiac tube of the embryo never retains its primitive longitudinal disposition in Craniates. Confined within the pericardium and attached at both ends, as it lengthens and thickens it necessarily bends and becomes somewhat spirally coiled. A ventral V-shaped loop to the right involving the ventricular and bulbar regions and directed backwards is constantly formed, and the whole tube acquires an S-shaped curve. The atrium thus comes to lie dorsally to the ventricle whose apex points backwards.
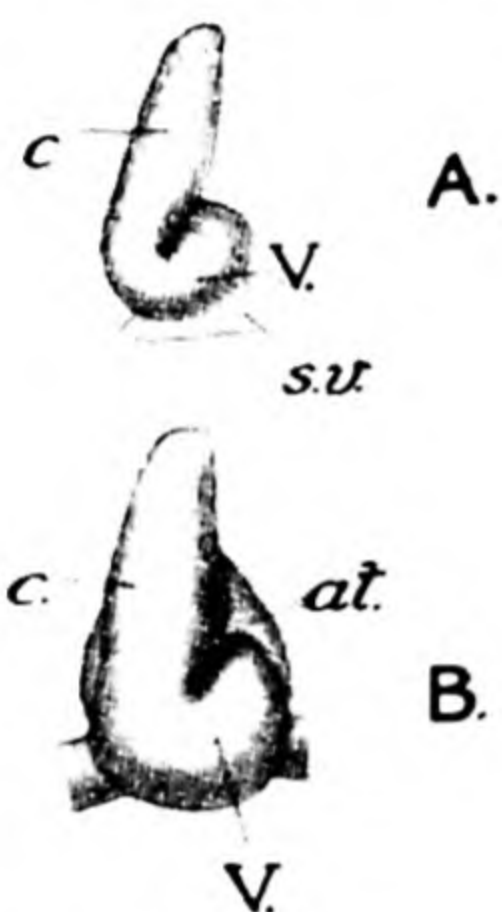
FIG. 553.

Two stages in the development of the heart of *Squalus* seen from the ventral side. (After Hochstetter, 1906.) *at*, Atrium; *c*, conus arteriosus; *s.v*, sinus venosus; *V*, ventricle. (From Kerr, *Embryology*, 1919.)

This curvature of the heart is more pronounced in higher than in lower forms, Figs. 553, 560, 572.

Coming now to the modifications of the heart in the various groups of fishes (Gegenbaur, 822-3 ; Röse, 862 ; Lankester, 843 ; Parker, 853 ; Goodrich, 35 ; Daniel, 487 ; and others), we find the most primitive form in the Elasmobranchs, Figs. 553-5. Here the heart is outwardly almost bilaterally symmetrical and is enclosed in a roomy pericardial cavity. The large sinus, which receives the hepatic veins and ductus Cuvieri, has its opening into the still larger atrium guarded by two sagittal valves. Two obliquely set valves are also present at the atrio-ventricular aperture situated somewhat on the left side. The well-developed contractile conus developed from the bulbus cordis is usually provided with three main longitudinal rows (of which one is dorsal and two ventro-lateral) of many pocket valves set in transverse rows or tiers. The number of valves varies considerably, and there may be vestigial valves between the main ones. So many as six tiers of valves may be present ; those of the first tier are often enlarged, and those of the middle and posterior tiers may be reduced. A gap may occur between anterior and posterior tiers, as in *Heptanchus* ; in *Chimaera* and some sharks only two tiers of well-developed valves remain. These valves develop in the bulbus cordis from four longitudinal endocardial ridges capable of closing the lumen on contraction of the wall, and which later become subdivided and hollowed out into pockets directed forwards. Owing to the reduction of the ventral ridge only three well-developed valves usually

occur in each tier.[1] The conus leads into the elongated ventral aorta, which shows no differentiated truncus chamber.

The structure of the heart of the Teleostomi resembles that of the Elasmobranch, and has diverged from it chiefly in the region of the conus where important modifications occur, Figs. 555-6. The presence of a muscular contractile conus may be considered as a primitive feature (Gegenbaur, 823), and it persists in such lower Teleostomes as the Chondrostei, Polypterini, and Lepidosteoidei. That of *Acipenser*, with its three tiers of four or five valves, closely resembles the conus of Selachians; but in *Polypterus* and *Lepidosteus* it has become elongated and the number of valves greatly increased. *Lepidosteus* may have so many as seven longitudinal and eight transverse rows. On the contrary, in *Amia* and in the Teleostean series, as Gegenbaur showed, the conus tends to become reduced and replaced from in front by a non-contractile region with fibrous wall called the bulbus arteriosus. *Amia* has a large bulbus arteriosus, but still possesses a considerable conus with three tiers of four valves. In the typical Teleost, however, the conus has been practically abolished, being represented by at most a narrow muscular zone bearing a single row of valves rarely more than two in number. Intermediate con-

FIG. 554.

Heart of *Squalus acanthias*, from the dorsal side, with the atrium cut open. (After Röse.) *co, tr*, Truncus anteriosus; *D.C.d* and *D.C.s*, right and left precavals; *O.a.v*, atrio-ventricular aperture; *V.a.d* and *V.a.s*, right and left valve of the sinus venosus; *1a-4a*, afferent branchial arteries. (From Wiedersheim, *Comp. Anatomy*.)

ditions are found in some of the lower Teleosts (Clupeiformes); a distinct remnant of the conus with two transverse rows of valves occurs in *Albula* (Boas, 811), and also in *Tarpon* and *Megalops* (Senior, 868). Whether the Teleostean bulbus, which may acquire very thick fibrous walls, should be considered as a new formation, as a backward growth from the ventral aorta (truncus), or as a converted part of the conus itself, is doubtful. But in favour of the first view it should be said that there is little doubt that the surviving row of valves repre-

[1] The fact that four endocardial longitudinal ridges (right, dorsal, left, and ventral) occur in the embryonic heart not only of Elasmobranchii, Dipnoi, and Tetrapoda, but also of Acipenser, Amia, and Lepidosteus (E.S.G.), is evidence that the valves of the conus were originally disposed in four corresponding rows.
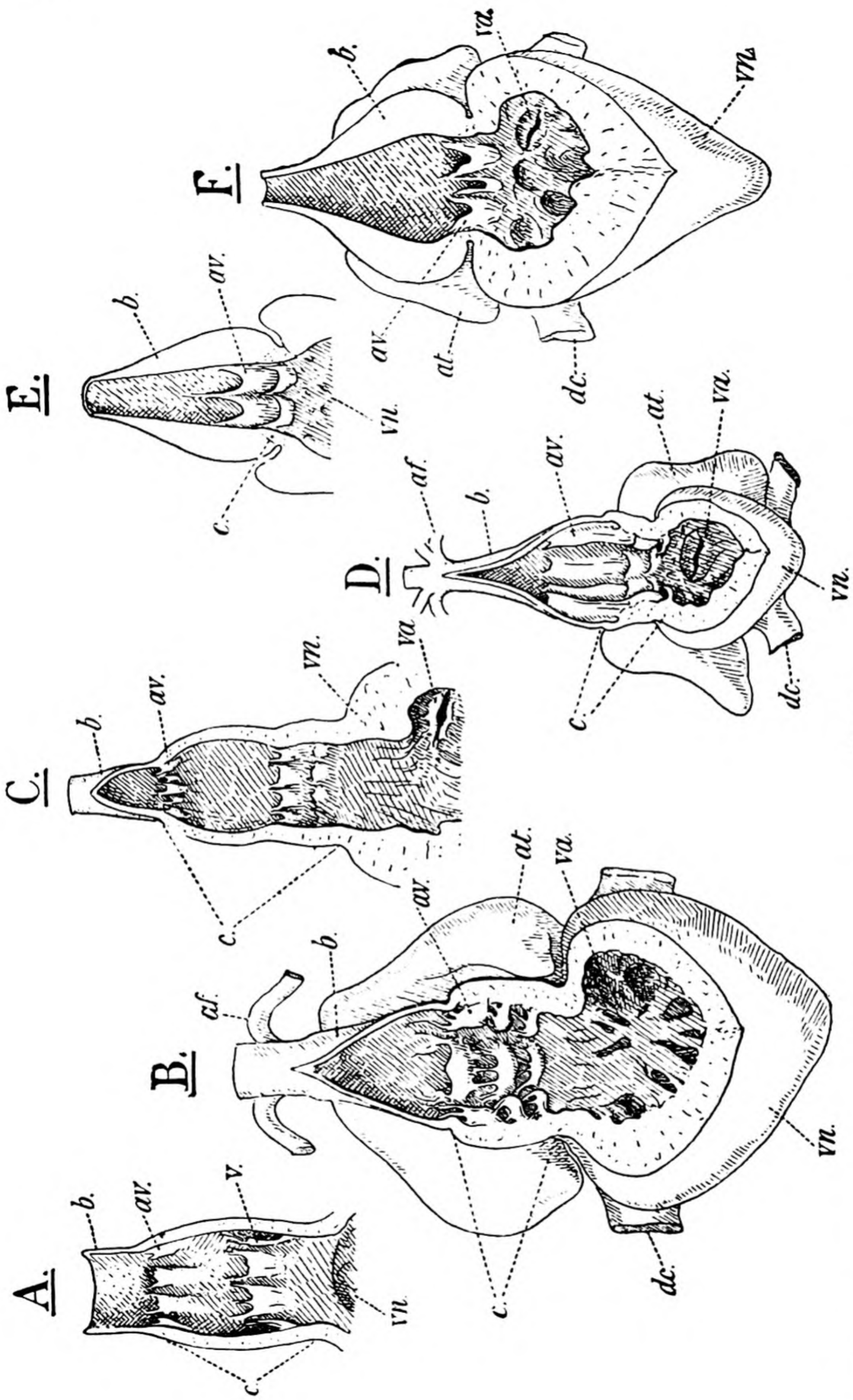
FIG. 555.

A, Conus arteriosus of *Chimaera monstrosa*, L.; B, heart of *Alopias vulpes*, Gm.; C, conus of *Acipenser sturio*, L.; D, heart of *Albula conorhynchus*, B. and E. (after Boas); F, heart of *Salmo salar*, L. Ventral view. *af*, Posterior afferent branchial vessel; *at*, atrium; *av*, anterior valve; *b*, base of ventral aorta which becomes the bulbus arteriosus in E and F; *c*, muscular contractile conus arteriosus which disappears in F; *dc*, ductus Cuvieri; *v*, posterior valve; *va*, atrio-ventricular aperture guarded by two valves; *vn*, ventricle. The bulbus conus and ventricle have been slit along the ventral mid-line, and stretched open to expose the valves. (From Goodrich, *Vert. Craniata*, 1909.)

sents the anterior and generally enlarged tier of more primitive forms, and Gegenbaur has pointed out that its valves are already attached in front to the wall of the truncus in Selachians. According to Senior and Hoyer (838) the conus is represented by the narrow muscle zone at the base of the valves which becomes joined to the Teleostean ventricle, and according to Hoyer and Smith the conus has been by a process of intussusception, so to speak, telescoped into the ventricle.

The Teleostean heart shows an extreme stage of specialisation peculiar to the group, and not leading to the structure of any of the higher vertebrates. This conclusion is amply supported by evidence derived from other organs such as the brain, alimentary canal, and gonads, all of which point to the Teleostei being a side branch of the phylogenetic tree.

The heart of Cyclostomes is in some respects highly specialised; chiefly perhaps owing to the strange fact, not yet explained, that only one ductus Cuvieri is preserved in the adult (J. Müller, 1833–43; Vialleton, 879; Röse, 862). The sinus venosus consequently takes up an almost vertical, dorso-ventral position, passing between atrium on the left and ventricle on the right. As Goette showed (825), the venous system develops normally in *Petromyzon* with paired ductus Cuvieri leading

FIG. 556.

Heart of *Lepidosteus osseus*, L. I, Ventral view; II, conus arteriosus opened. *a*, Atrium; *b*, conus; *e*, *f*, *g*, transverse rows of valves in conus; *h*, *k*, *l*, *m*, four afferent branchial vessels; *v*, ventricle. (After Günther, from Goodrich, *Vert. Craniata*, 1909.)

from paired cardinals to the sinus, which also receives blood from hepatic veins and a median jugular vein. Later an anastomosis develops dorsally between the right and left cardinals so that all their blood passes to the right ductus Cuvieri and the left ductus is obliterated. The sinus thus becomes a narrow vessel passing in the remaining portion of the meso-cardium to the right of the gut into the ductus above and into the jugular and hepatic veins below. The usual paired valves guard the sinu-atrial and the atrio-ventricular apertures. There is no well-developed conus; but this chamber is represented by a short region beyond the ventricle,

containing in *Petromyzon* two longitudinal ridges comparable to those found in the embryonic conus of other forms (Vialleton). The passage
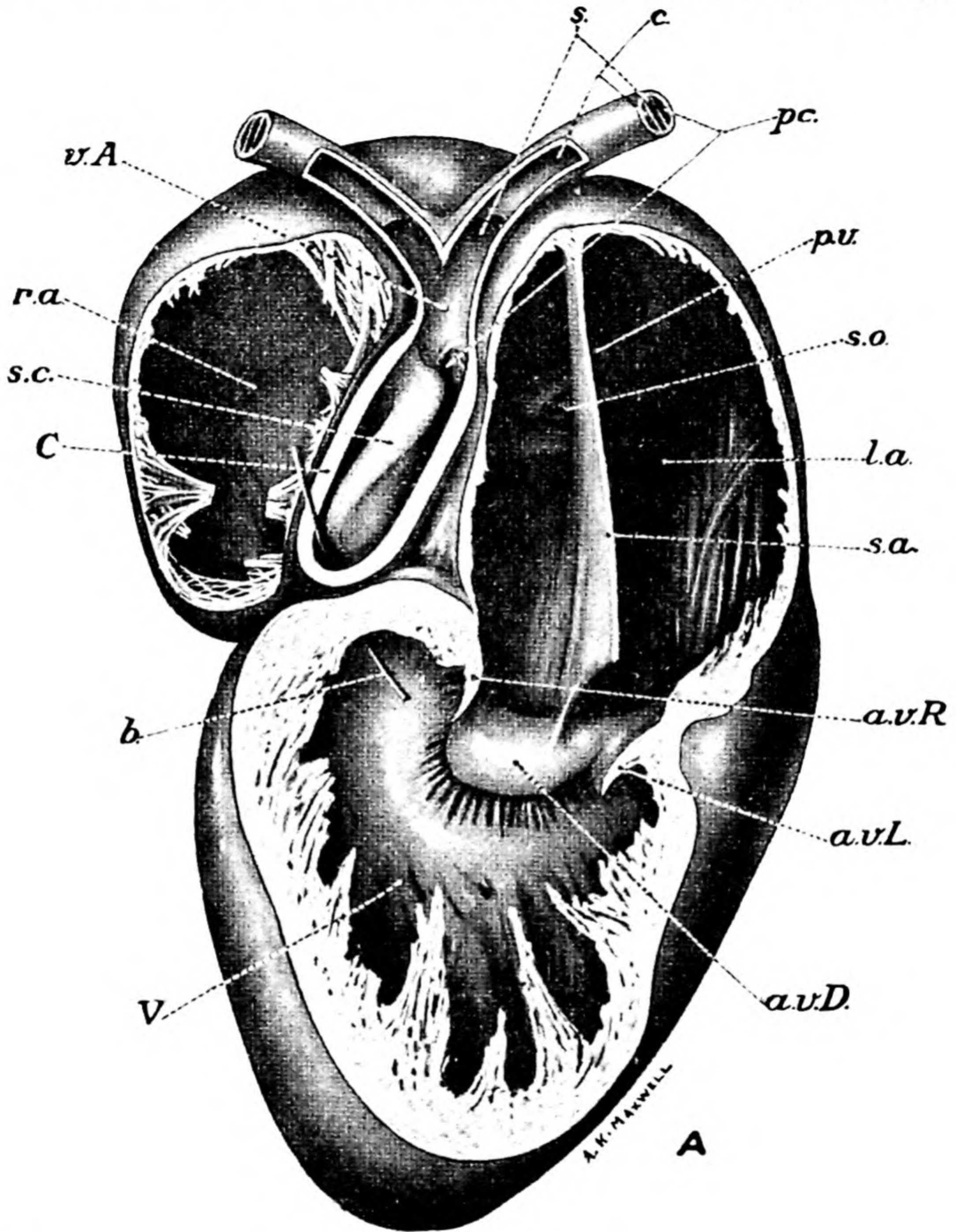
FIG. 557.

Heart of the frog. A, General dissection from the ventral side. *a.v.d*, Dorsal atrio-ventricular valve ; *a.v.L*, left ditto ; *a.v.R*, right ditto ; *b*, bristle passed from ventricle into conus ; *C*, conus ; *c*, carotid ; *l.a*, left auricle ; *p.v*, opening of pulmonary vein ; *pc*, pulmo-cutaneous ; *r.a*, right auricle ; *s*, systemic cavity ; *s.a*, atrial septum ; *s.c*, septum of conus ; *s.o*, opening from sinus venosus ; *V*, ventricle ; *v.A*, ventral aorta. (From J. G. Kerr, *Zoology*, 1921.)

from the ventricle to the conus is provided with a right and left pocket valve. A remarkable fact is that, while it is the right ductus Cuvieri which alone persists in the adult Lampreys, it is the left ductus which is preserved in Myxinoids, Figs. 521, 680*a*.

Leaving for the present the consideration of the Dipnoan heart and passing to the Tetrapods, we find a general advance in specialisation, and a profound modification correlated with the appearance of pulmonary respiration and the disappearance of the gills. Already in the Amphibia, more especially in Anura, the heart acquires the shape characteristic of this organ in Tetrapods (Boas, 813 ; Gaupp, 821 ; Röse, 862 ; Rao and Ramana, 857 ; Rau, 858 ; Oliver, 1910). Moreover, the pericardial wall becomes thinned out and freed from the lateral body-wall, so that the heart is covered by a thin membrane extending above, behind, and at the sides, Figs. 552, 557-8. In the Anuran heart the S-shaped curvature is so pronounced that the atrium (auricles) is carried forwards in front of the large and very muscular ventricle and now opens backwards into it. The sinus venosus is also carried forwards dorsally and opens downwards into the atrium. An important innovation is the subdivision of the atrial cavity into a large right and smaller left auricle by an interauricular septum, a sagittal fold first arising from the anterior wall and extending posteriorly and to the auricular ventricular aperture. The oxygenated blood is brought directly from the lungs to the left auricle by a special pulmonary vein passing over the sinus. The sinus itself, still a nearly bilaterally symmetrical cavity formed by the junction of the two ductus Cuvieri and vena cava inferior, receives the venous blood from the rest of the body (and from the heart by the coronary vein) and pours it into the right auricle through an opening protected by right and left semilunar valves. The openings of the pulmonary vein and of the sinus are on opposite sides of the septum. Two large dorsal and ventral and two small right and left valves guard the single opening from the auricles to the ventricle. The spirally twisted conus is much specialised. The region of the embryonic bulbus cordis becomes in adult Anura differentiated into a posterior conus (pylangium) and short anterior 'truncus impar' (synangium). The latter passes outside the pericardium into right and left branches, each of which soon splits into the three anterior arches. That the conus with its contractile wall provided with striated muscle belongs to the heart there can be no doubt ; but the anterior part or perhaps the whole of the truncus impar should be reckoned as representing the shortened ventral aorta. As usual the bulbus cordis is provided in the embryo with four longitudinal (spiral) internal endocardial ridges which give rise to valves. The dorsal, left, and ventral ridges are interrupted in the middle and give rise as a rule only to three pocket valves at the anterior end and three or fewer at the posterior end of the conus with a wide gap between. The better-developed right ridge becomes a continuous longitudinal fold (septum bulbi, spiral

valve) projecting into the lumen so as to subdivide it incompletely into two channels—the cavum systemo-caroticum and cavum pulmo-cutaneum. Attached anteriorly to the dorsal surface of the conus wall, this fold turns to the left and ends posteriorly on the ventral surface near the ventricular opening. At its anterior end it expands to a hollow pocket-like valve, into which penetrates the extreme posterior end of the horizontal septum of the truncus (septum principale). This fold completely separates the lumen of the truncus into a dorsal passage continuing the cavum pulmo-cutaneum and a ventral passage continuing the cavum systemo-caroticum. Shortly in front of the anterior conus valves the
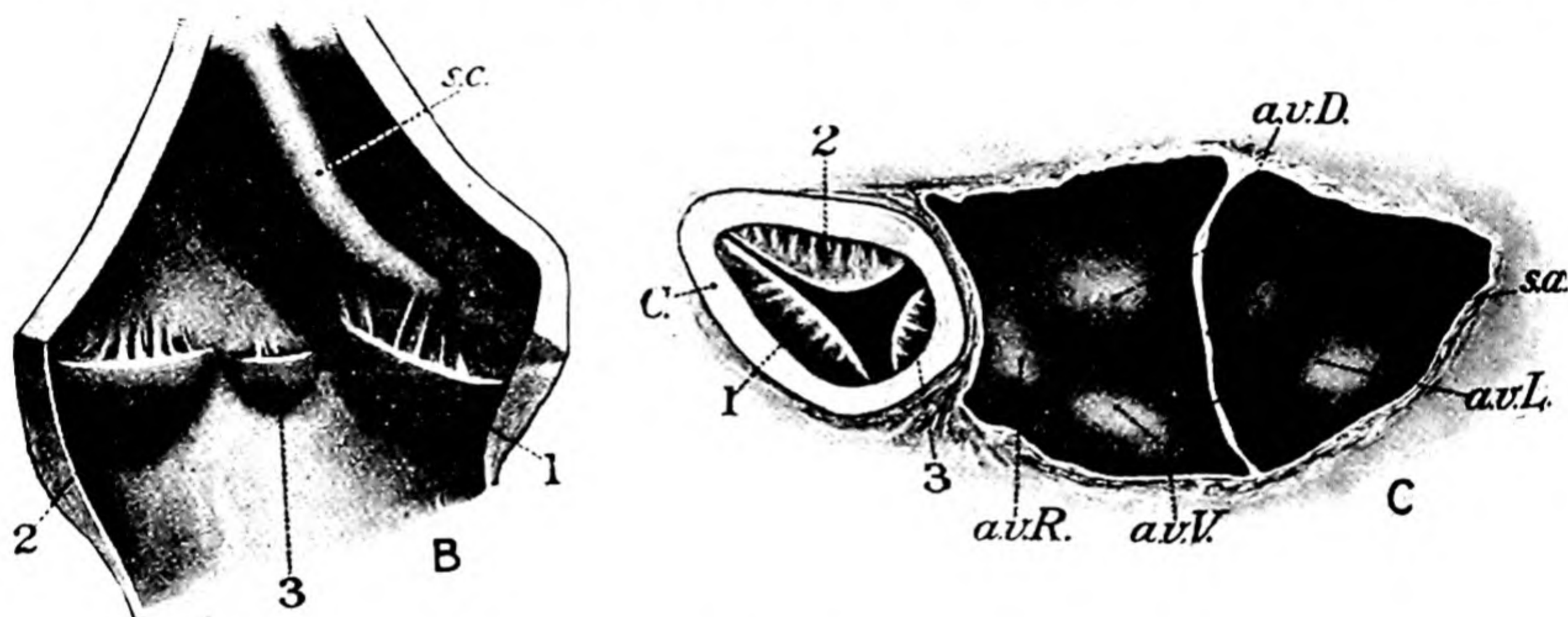
FIG. 558.

Heart of a frog. B, Ventricular end of conus slit open to show the pocket valves; C, atrio-ventricular valves (closed), etc., as seen in a heart cut transversely through the auricles and conus and viewed from the headward side. *a.v.D*, Dorsal atrio-ventricular valve; *a.v.L*, left ditto; *a.v.R*, right ditto; *a.v.V*, ventral ditto; *C*, conus; *s.a*, atrial septum; *s.c*, septum of conus; 1, 2, 3, pocket valves at ventricular end of conus. (From J. G. Kerr, *Zoology*, 1921.)

latter passage is again subdivided into paired systemic and carotid cavities leading to their respective arches. These various septa, subdividing the cavity of the truncus, including the septum principale, appear to be formed by the extension backwards of the walls separating the approximated bases of the arches. Concerning the exact mode of action of this complicated system of folds, valves, and septa, there is still some difference of opinion (Sabatier, 865; Gaupp, 821; Rau, 858); but the main result seems to be as follows. The venous blood received by the right auricle passes into the ventricle whence it is forced up the cavum pulmo-cutaneum, and the aerated blood, brought to the left auricle from the lungs, is passed through the ventricle and driven up the cavum systemo-caroticum. The arterial and venous streams are but little mixed in the ventricle owing to the sponginess of its wall, and to the bulk of the venous blood being expelled in the first phase of ventricular contrac-

tion and of the purest arterial blood in the last phase of contraction. The anterior pocket valves help to distribute the blood to the several passages in the truncus; and thus, while the carotid arch receives the purest arterial blood and the pulmonary the most venous, the systemic supply is somewhat mixed. But the blood may be oxygenated not only in the lungs but also in the buccal cavity and in the skin supplied by the cutaneous branch of the pulmonary arch (p. 524), so that the circulation
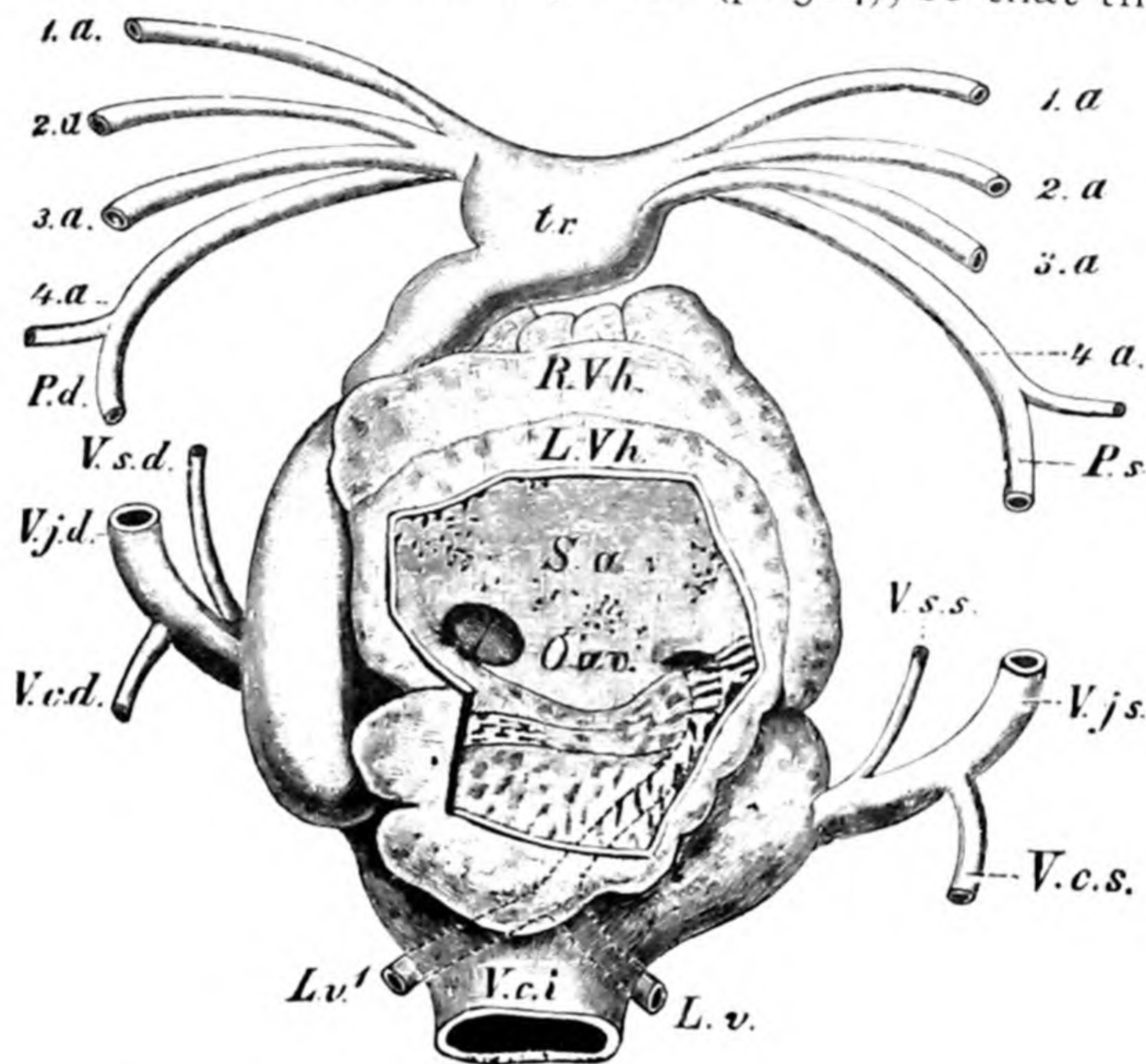
FIG. 559.

Heart of *Cryptobranchus japonicus.* From the ventral side. (After Röse.) The left auricle is cut open. *L.v, L.v¹,* The two pulmonary veins, opening by a single aperture into the left auricle; *L.Vh, R.Vh,* left and right auricles; *O.av,* atrio-ventricular aperture; *P.d* and *P.s,* left and right pulmonary arteries; *S.a,* septum atriorum, perforated by numerous small apertures; *tr,* truncus arteriosus; *V.c.d, V.c.s,* posterior cardinal veins; *V.c.i,* postcaval vein; *V.j.d* and *V.j.s,* jugular veins; *V.s.d* and *V.s.s,* subclavian veins; 1a, 4a, the four arterial arches. (From Wiedersheim, *Comp. Anat.*)

fulfils its purpose in spite of the incomplete separation of the two streams in the heart.

In the structure of the heart, as in so many other respects, the Urodela are somewhat degenerate or retain certain larval characters, Fig. 559. While the sinus venosus, auricles, and ventricle resemble in general those of the Anura, the heart is less compact and the conus is usually much simpler (Boas, 813). The terrestrial *Salamandra* preserves the pocket valves and longitudinal spiral valve much as in the frog, but the horizontal septum of the truncus is not so much developed, does not grow backwards so far into the conus. The lumen of the truncus is subdivided into four paired channels corresponding to the four pairs of persistent arches. In the more aquatic Urodela the tendency is for the conus to

remain undeveloped, and for the spiral valve to disappear more or less completely. Thus *Siren* has four posterior pocket valves and three anterior, with a fourth elongated into a short spiral fold ; but in *Meno-*
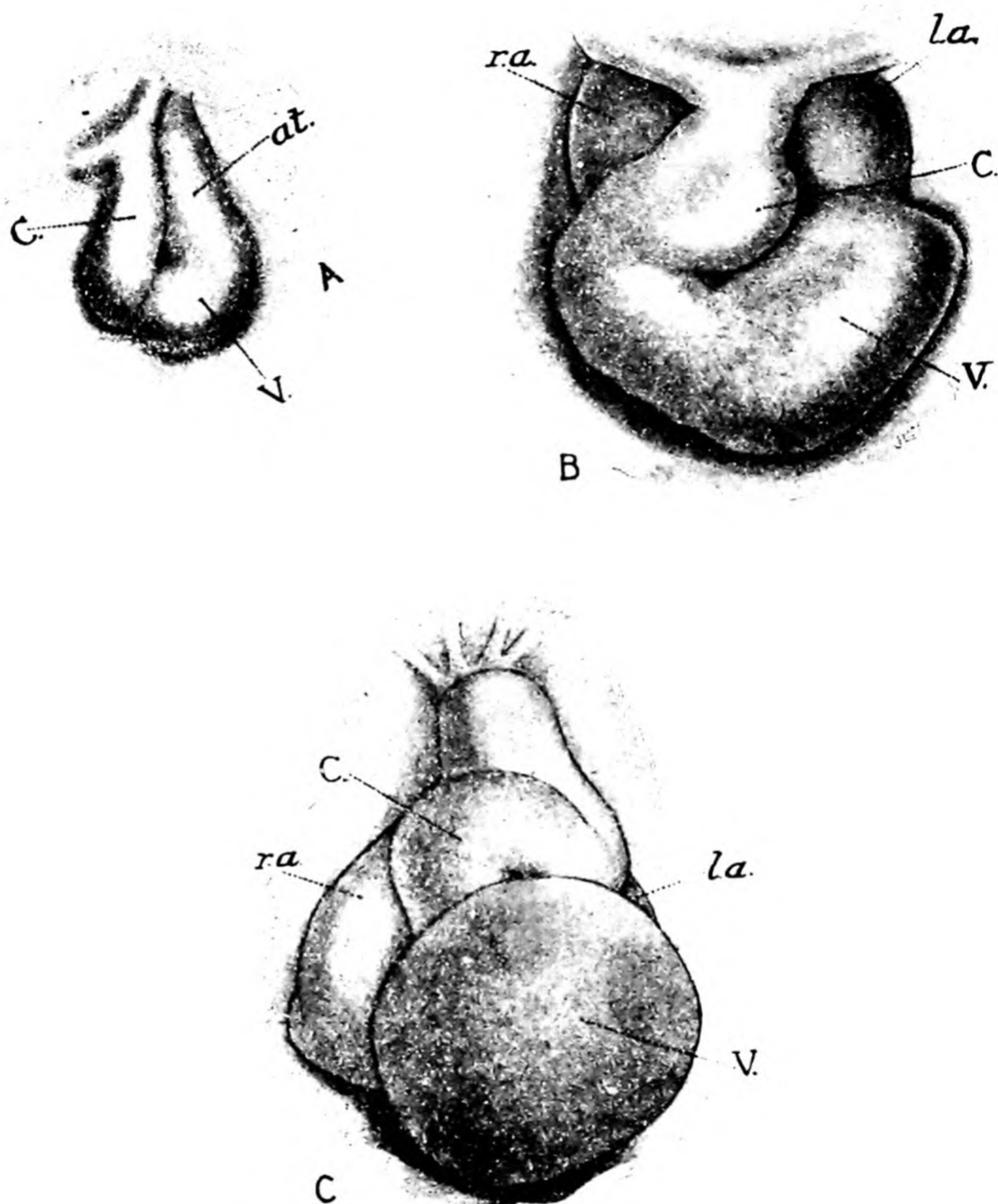
FIG. 560.

Views of the heart of *Lepidosiren* as seen from the morphologically ventral side. (B and C after J. Robertson, 1913.) A, Stage 32 ; B, stage 31 ; C, stage 35. *at*, Atrium ; *C*, conus arteriosus ; *l.a*, left auricle ; *r.a*, right auricle ; *V*, ventricle. (From Kerr, *Embryology*, 1919.)

branchus the spiral fold has disappeared leaving only four main pocket valves at each end of the conus, and in *Proteus* only two pairs of such valves are present. Moreover, the interauricular septum is thin and often perforated. Thus the venous and arterial streams become less completely separated, and it is clear that the heart tends to lose its specialisa-

tions as the branchiae remain more and more functional in the adult, and pulmonary respiration loses its importance. The same sort of degeneration occurs in the Gymnophiona (Apoda) where cutaneous respiration is so much developed ; for here also the spiral fold disappears, and even the posterior valves of the conus (Wiedersheim, 652 ; Boas, 813). In the aberrant lungless Salamanders, indeed, not only may the conus be simplified, but the interauricular septum may not be developed, a return to an almost fish-like condition (Bruner, 816 ; Hopkins, 387).

The study of the heart of the Dipnoi is of great importance for the understanding of the structure and phylogeny of the heart in the Tetrapoda
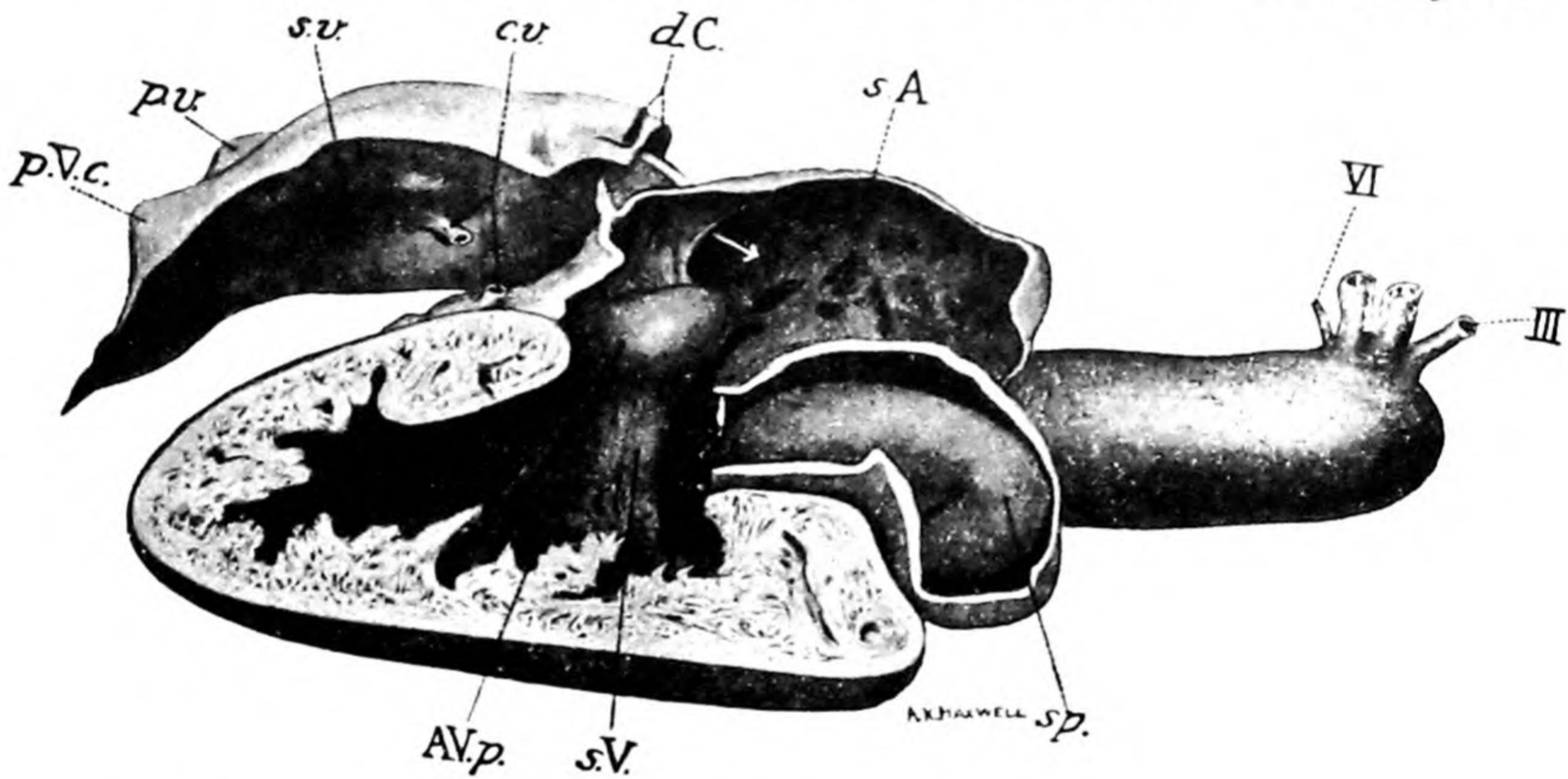
FIG. 561.

Heart of an adult *Lepidosiren* with the right side removed. (After J. Robertson, 1913.) *AV.p,* Atrioventricular plug ; *c.v,* coronary vein (cut) ; *d.C,* ducts of Cuvier ; *p.v,* pulmonary vein ; *p.V.c,* posterior vena cava at its opening into the sinus venosus ; *s.A,* atrial septum ; *s.V,* ventricular septum ; *s.v,* sinus venosus (its opening into the right auricle indicated by an arrow) ; *sp,* spiral valve ; III, VI, aortic arches cut near their ventral ends. (From Kerr, *Embryology.*)

(Boas, 812 ; Röse, 862 ; Robertson, 861 ; Kerr, 840 ; Goodrich, 35). The heart lies in a pericardial cavity behind the gills and still bounded by stiff walls. The curvature is more pronounced than in other fishes, and although the sinus venosus still starts near the posterior pericardial wall it lies to a great extent dorsally to the ventricle whose apex projects far back below it. The atrium is brought far forwards above the ventricle and base of the conus and opens downwards into the ventricle, Figs. 560-64. Thus the heart approaches in shape that of the Urodele Amphibian. The sinus venosus receives the venous blood from two ductus Cuvieri and a median vein formed by the union of a vena cava inferior with the hepatic veins ; but an important new departure is the separation of the return stream from the lung-like air-bladder. For the

two pulmonary veins join, as in Amphibia, to a single vessel which, passing along the dorsal wall of the sinus, empties aerated blood directly into the left side of the atrium. Into the right side of the atrium the sinus empties the venous blood, and there extends from behind and above a muscular septum which subdivides the atrial cavity almost completely into larger right and smaller left auricular spaces. Immediately to the right of this interauricular septum is the sinu-auricular opening provided with a right valve, and on the left side of the septum is the opening of the pulmonary vein protected by a small fold on the left. Into the large atrio-ventricular opening fits a fibrous or partly cartilaginous plug arising from the posterior
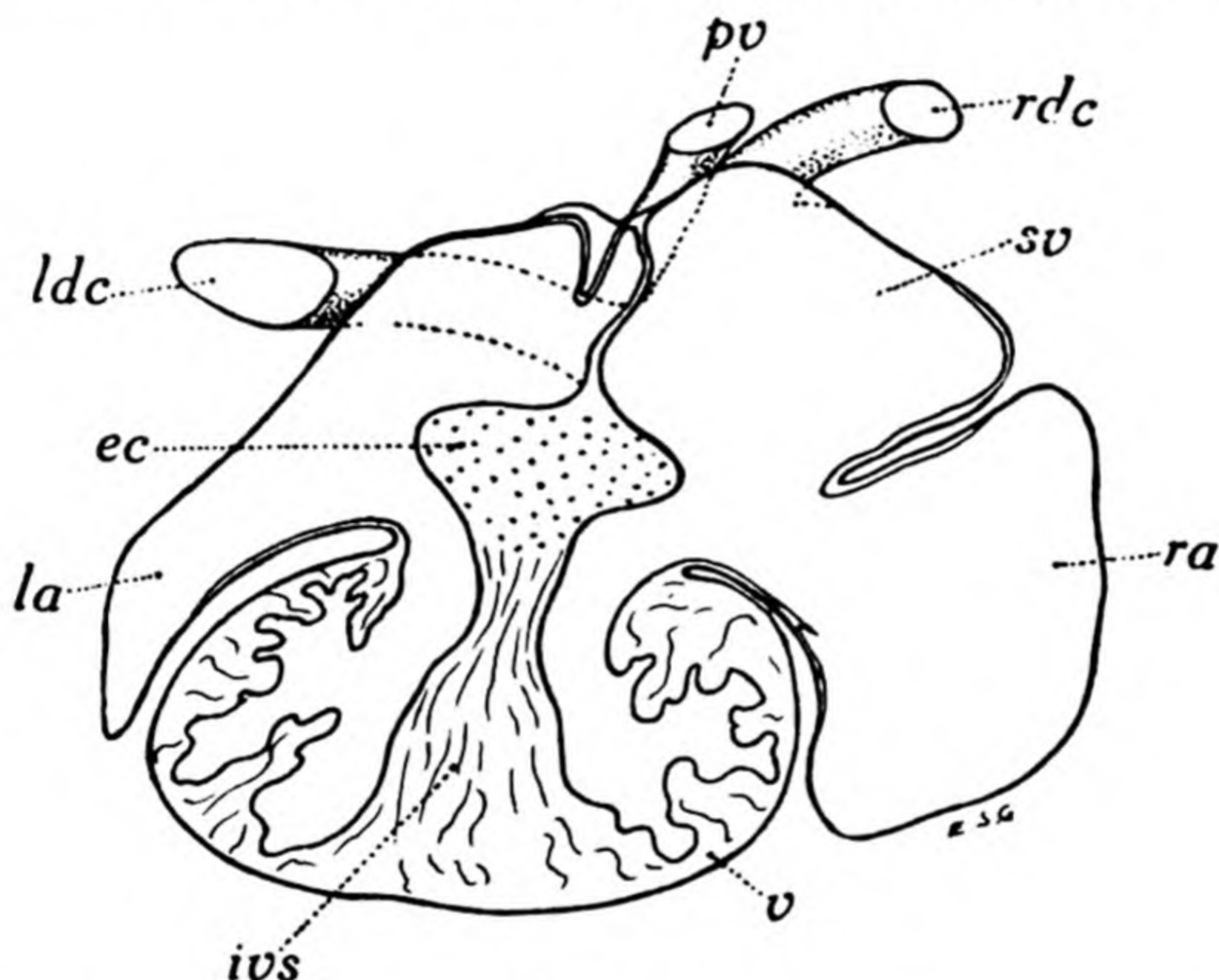
FIG. 562.

Protopterus annectens, transverse section of heart of larva through auriculo-ventricular openings. *ec*, Endocardial cushion ; *ivs*, interventricular septum ; *la*, left auricle ; *ldc*, left ductus Cuvieri ; *pv*, pulmonary vein ; *ra*, right auricle ; *rdc*, right ductus Cuvieri ; *sv*, sinus venosus ; *v*, ventricle.

margin of the opening. This highly characteristic structure is peculiar to the Dipnoi ; it is attached above to the interauricular septum and below to a corresponding median ventral muscular interventricular septum which incompletely subdivides the ventricular cavity from behind. By means of these muscles the plug can be raised to open or lowered to close the aperture into the ventricle. No other valves are developed at the atrio-ventricular opening, and the plug probably represents an enlargement of the ventral of the two endocardial cushions here developed in other forms, Fig. 562.

The large conus, developed from the bulbus cordis, has but feebly developed musculature anteriorly and a marked spiral twist. Robertson describes the development in the bulbus cordis of *Lepidosiren* of four longitudinal ridges interrupted in the middle region and sharing in the

spiral twist.[1] From these arise the valves and ridges of the adult conus. The dorsal and ventral ridges are vestigial; posteriorly they give rise to vestigial pocket valves round the base of the conus. The right main ridge becomes continuous and develops into the 'spiral valve', which meets and even fuses anteriorly with the opposing shorter left ridge. These two ridges meeting subdivide the lumen of the conus in front into dorsal and ventral channels (as in Amphibia). Since the hinder end of the right ridge thus passes to the left and becomes ventral, owing to the spiral twist, it continues the line of the interventricular and interauricular septa. Thus the cavity of the whole heart is incompletely divided longitudinally into two channels. The venous stream on the right is driven mainly into the dorsal channel, and the arterial stream on the left into the ventral channel of the anterior region of the conus. In this way the first two adult arterial arches, with which are connected the carotid arteries, are supplied mainly with arterial blood; while the more venous blood passes to the remaining arterial arches, including the last which gives

FIG. 563.

Ceratodus Forsteri, Krefft. Ventral view of the heart dissected so as to expose the inside of the ventricle and conus, and the disposition of the aortic arches. a^{1-4}, Four aortic arches (a dotted line passes up the base of the 1st and combined 3rd and 4th); at, atrium; c, cut wall of conus; f, plug filling the atrio-ventricular opening; lv, small posterior valves; p, portion of wall of pericardium; sv, specialised row of enlarged valves; t, truncus; v, anterior valve; vt, cut wall of ventricle; w and z, dotted lines passing into the sinus venosus. (Compare Fig. 564, p. 552.) (From Goodrich, Vert. Craniata, 1909.)

off the pulmonary artery (p. 583). For the ventral aorta of Dipnoi is

[1] The apparent spiral twist of this region in Dipnoi and Tetrapoda is associated with the kinking of the elongating tube (Kerr, 840; Bremer, 815).

shortened up into a truncus remarkably like that of Amphibia, and as in the latter the walls between the arches are carried back so as to sub-
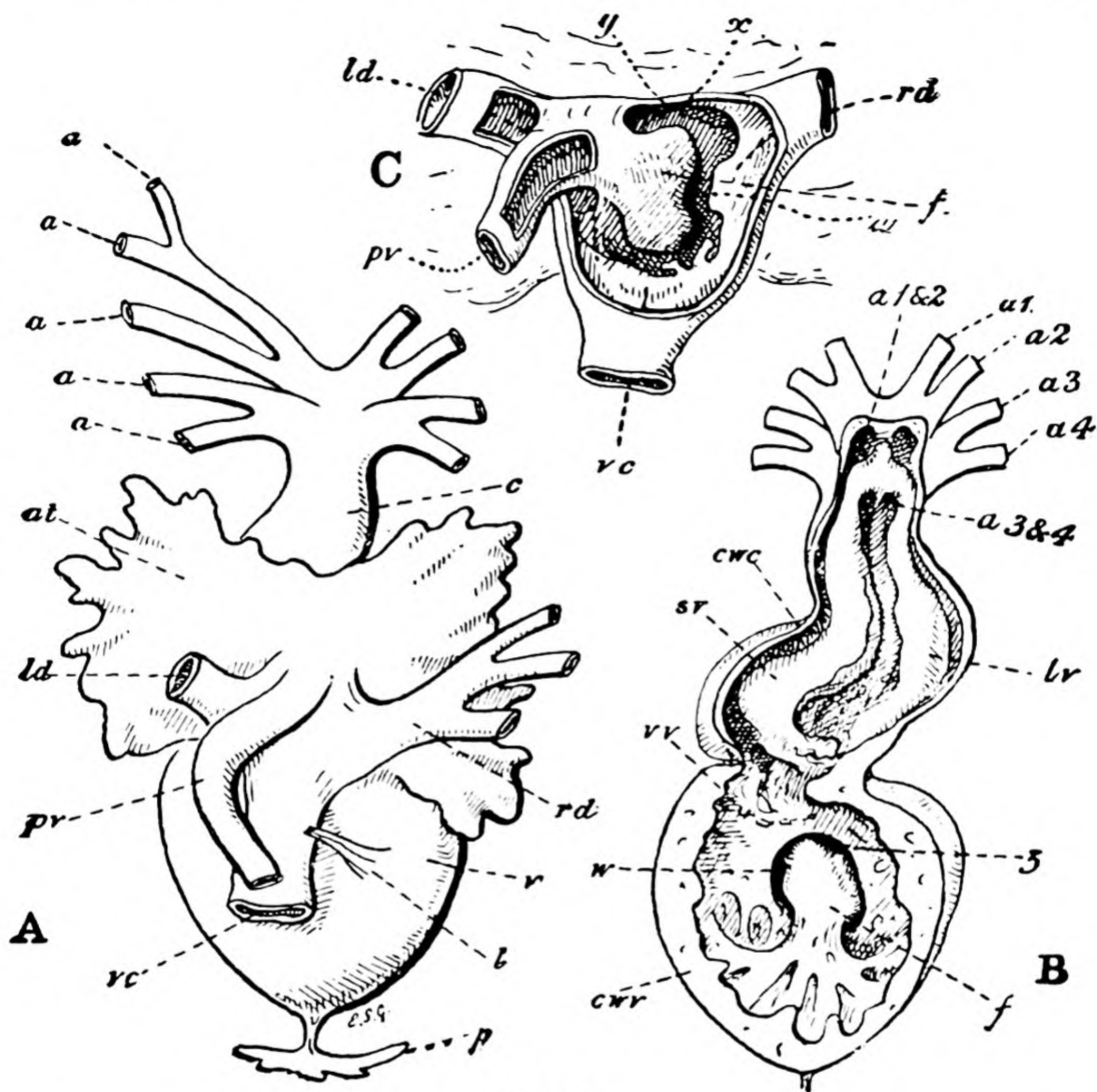
FIG. 564.

Heart of *Protopterus annectens*, Owen. A, Dorsal view; B, opened, ventral view; C, the sinus venosus opened. *a*, Cut arterial arches; *a* 1 and 2, entrance from conus to first two arches; *a* 3 and 4, entrance to last two arches; *at*, atrium; *c*, conus arteriosus; *cwc*, cut wall of conus; *cwv*, cut wall of ventricle; *f*, fibrous plug closing the passage from ventricle to atrium and passing into the sinus; *l*, dorsal attachment to pericardial wall; *ld*, left ductus Cuvieri; *lv*, longitudinal ridge; *p*, small portion of pericardial wall; *pv*, pulmonary vein; *rd*, right ductus Cuvieri; *sv*, longitudinal compound valve; *v*, ventricle; *vc*, vena cava inferior; *vv*, row of small valves; *w*, dotted line indicating course of venous blood from the shallow sinus venosus, through the atrium (C) into the ventricle on the right of the plug (B). In C the dotted lines *ld*, *rd*, and *vc* pass into the sinus venosus; the lines *x* and *y* into the cavity of the atrium opening widely into the sinus; the line *pv* passes down the pulmonary vein to enter the ventricle on the left of the plug (*z* in B). (From Goodrich, *Vert. Craniata*, 1909.)

divide its lumen into three paired channels: two ventral leading to adult arches 1 and 2, and one dorsal leading to arches 3 and 4 on each side.

There is, then, a very striking resemblance in the structure of the heart and truncus of the Dipnoi and Amphibia, which cannot be put down entirely to convergence, and clearly points to the development of

a similar structure in their common ancestor when still at an aquatic and fish-like stage. Nevertheless, to some extent the resemblance may be due to convergence; for *Ceratodus*, the most primitive of living Dipnoi, has a less specialised heart than *Lepidosiren* or *Protopterus*. For instance, in *Ceratodus* the valves of the conus are more numerous, regular, and less fused into ridges; they are more like the valves of the Selachian conus. There are anteriorly four longitudinal rows of valves, of which the first tier is enlarged, and a gap separates the second tier from the four posterior tiers of numerous small valves in three of the rows.

The main right longitudinal row is continuous and spiral, but its constituent six valves are not fused into a ridge. The tendency to form longitudinal ridges is more pronounced and the interventricular and interauricular septa are more developed in the specialised Dipneumones than in *Ceratodus*. In these respects, then, some of the Dipnoi have probably advanced beyond the level of specialisation reached by the ancestor common to them and the Tetrapoda. Indeed, although an interventricular septum reappears in all Amniota, it is very doubtful whether it is a common ancestral structure, since it is not found in any modern Amphibian.

The Amniote heart reaches an altogether higher grade of specialisation than the Amphibian. Even in the lower

FIG. 565.

Heart of *Cyclodus boddaertei*. From the dorsal side. (After Röse.) *An, An.s,* Innominate arteries; *Ao.abd,* dorsal aorta; *D.C.d, D.C.s,* precaval veins; *L.v,* pulmonary vein; *P.s, P.d,* pulmonary arteries; *Sp.i,* spatium intersepto valvulare; *V.C.d,* posterior cardinal; *V.j.d,* jugular, and *V.s.d,* subclavian vein of the right side; *V.c.i,* postcaval vein. (From Wiedersheim, *Comp. Anatomy.*)

forms it is more compact, with the auricles carried forwards on to the anterior surface of the large conical ventricle, and the reduced sinus venosus on to the dorsal surface of the auricles, so that the bases of the arterial arches and great veins come nearer together, Figs. 552, 571-2. The sinus tends to disappear during development, being flattened and more or less merged, as it were, into the wall of the right auricle. An important advance, usually not sufficiently noticed, is the disappearance of the conus as such in all Amniotes. For the cavity of the bulbus cordis becomes subdivided by a longitudinal spiral septum down to its base, so that completely separated pulmonary and aortic channels are formed with separate openings, provided with semilunar pocket valves, into the ventricle (or ventricles). The former channel opens

backwards towards the right and the latter towards the left. The wall of this region ceases to be contractile, loses its striated musculature, and becomes fibrous like that of the large arteries with which it is continuous. Furthermore, except in some of the smaller and lower Reptiles,

FIG. 566.

Heart of a young *Crocodilus niloticus*. From the dorsal side (after Röse). *A.d* and *A.s*, Right and left aortic arches; *A.m*, mesenteric artery; *L.V.h*, *R.V.h*, left and right atria; *S.d*, *S.s*, subclavian arteries; *Tr.cc*, common carotid; *V.cc*, coronary vein; *D.C.d*, *D.C.s*, precaval veins; *L.V*, pulmonary vein; *P.s*, *P.d*, pulmonary arteries; *Sp.i*, spatium intersepto-valvulare; *V.c.i*, postcaval vein. (From Wiedersheim, *Comp. Anatomy*.)

the whole conus region becomes so completely subdivided that it is split into two separate tubes or trunks, of which the pulmonary trunk passes forwards ventrally to the left round the aortic trunk, and then dorsally to the lungs.

The development of the Amniote heart has been much studied; among recent writers one may consult Langer (841-2), Hochstetter (835-6), Greil (831) for Reptiles and other Amniotes; Masius (847), Greil (831), Fuchs (820) for Birds; Lockwood (1888), Röse (862), Born (1888-9), Langer (842), Tandler, and others for Mammals. It may here be mentioned that the bulbus in Mammals, and perhaps also in other Amniotes, seems to contribute to the wall of the definitive right ventricle, and that longitudinal endocardial ridges (typically four in number) develop in it as in other Craniates. The semilunar valves at the base of the large vessels are derived from their posterior ends, while the dividing septum mentioned above is first formed by the meeting across and fusion of the right and left ridges. This septum pulmo-aorticum, then, may be compared to the spiral folds of Amphibia and Dipnoi described above.

Another very important new feature is the formation of a septum

more or less completely subdividing the cavity of the ventricle into right and left chambers. Already in Amphibia the venous and arterial
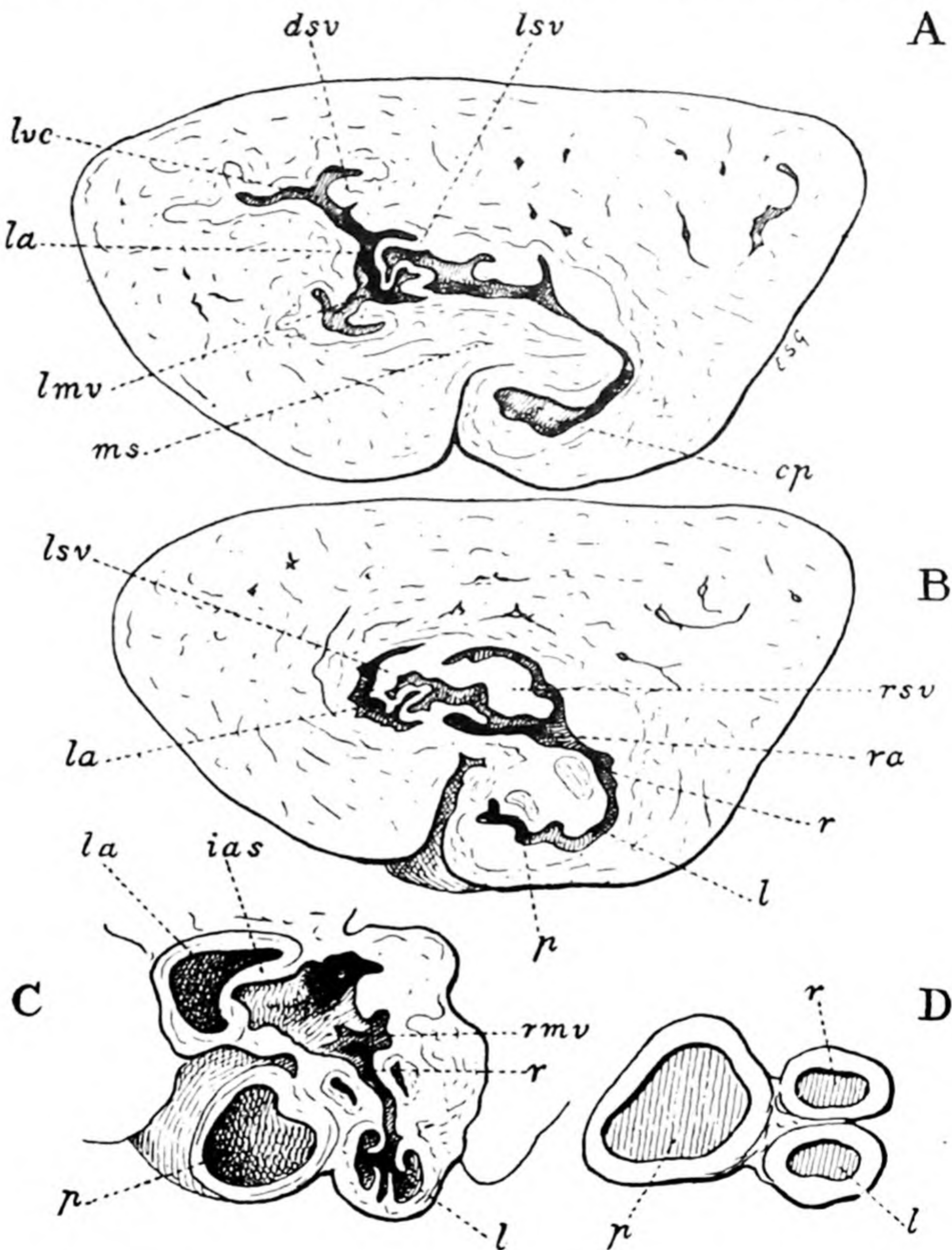
FIG. 567.

Chelone midas. Successive transverse sections through ventricle and base of aortic arches seen from behind (posterior view) with dorsal edge above and ventral edge below. A, Most posterior, and D, most anterior section. *cp*, Cavum pulmonale ; *dsv*, muscles representing dorsal region of interventricular septum ; *ias*, interauricular septum ; *l*, left aortic arch ; *la*, left auriculo-ventricular opening ; *lmv*, left auriculo-ventricular marginal valve ; *lsv*, left septal (medial) auriculo-ventricular valve ; *lvc*, left ventricular chamber ; *ms*, incomplete muscular interventricular septum ; *p*, pulmonary trunk ; *r*, right aortic arch ; *ra*, right auriculo-ventricular opening ; *rmv*, right auriculo-ventricular marginal valve ; *rsv*, right septal (medial) auriculo-ventricular valve ; *v*, ventricle. (Figs. 567-70 and 580, from Goodrich, *J. of Anat.*, 1919.)

blood-streams are separated so far as the ventricle by an interauricular septum, but it is not until the higher Amniota that the separation already foreshadowed in Dipnoi is at last accomplished by a similar partition in the ventricle.

An interesting point of great phylogenetic significance and not usually appreciated is that this has been completed along two independent divergent lines—the Sauropsidan leading to Birds and the Theropsidan leading to Mammals (see further, below, p. 572).

In Reptiles, though already considerably reduced in size, the sinus is usually quite distinct internally, Figs. 565-6. The right ductus Cuvieri
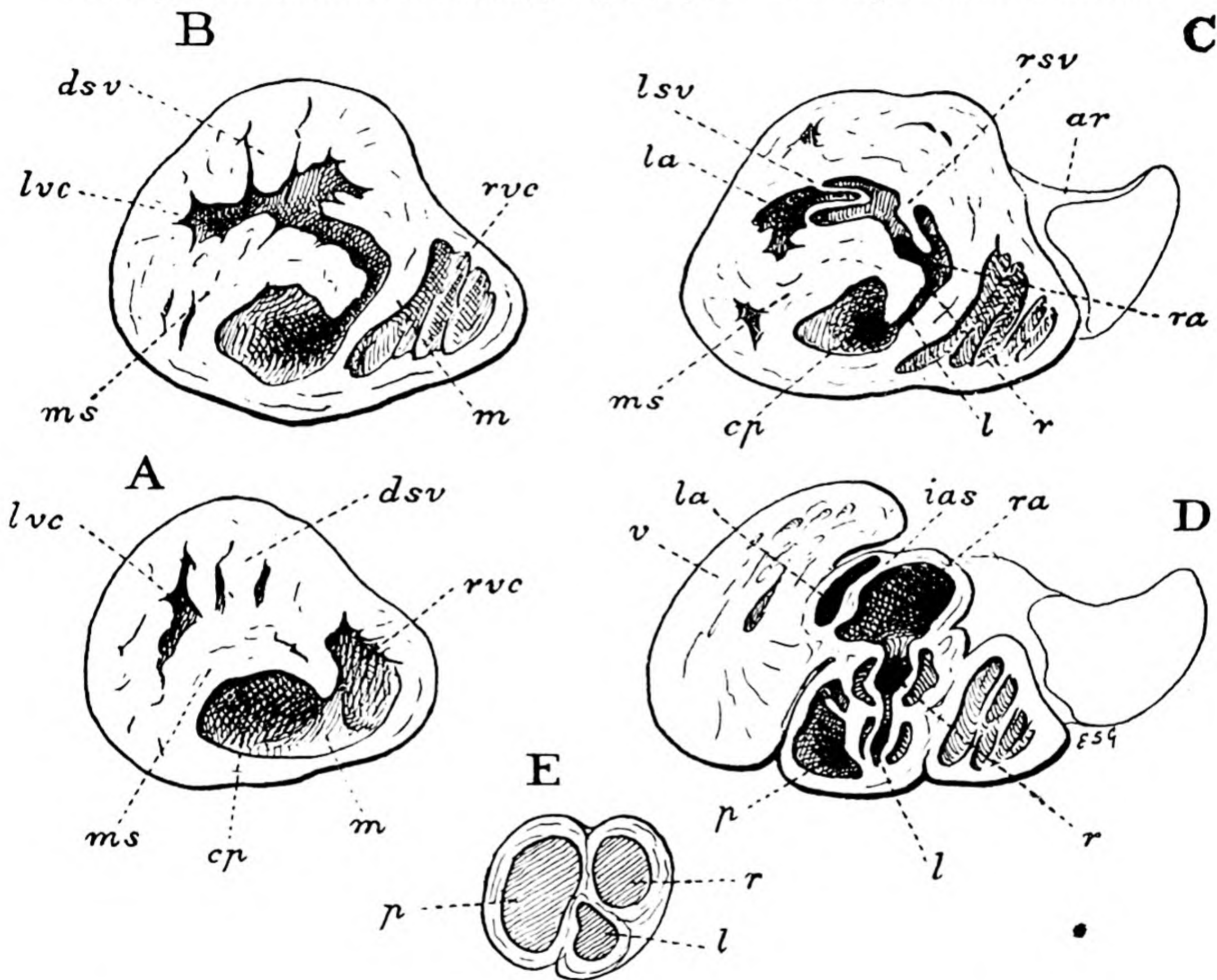
FIG. 568.

Varanus sp. Successive transverse sections through heart, seen from behind. A, Most posterior, E, most anterior section. Lettering as in Fig. 567.

(anterior vena cava dextra) tends to open anteriorly to the vena cava inferior, and the left ductus (ant. vena cava sinistra) passes across to open near the latter. A partial septum sinu-venosi may arise from the wall between these two openings and that of the right ductus. The well-developed valves guarding the sinu-auricular opening into the right auricle are set almost transversely, one anterior and one posterior. In the Reptilian heart, then, the sinus opens into the larger right auricle and the pulmonary vein into the smaller left auricle, and these two cavities are separated

by an interauricular septum always complete in the adult, but pierced by secondary temporary perforations in the embryo which are closed when pulmonary respiration is established (such perforation also occurs in Birds and Mammals).

Along the free edge of this interauricular septum crossing the atrio-ventricular opening are attached two membranous valves projecting into
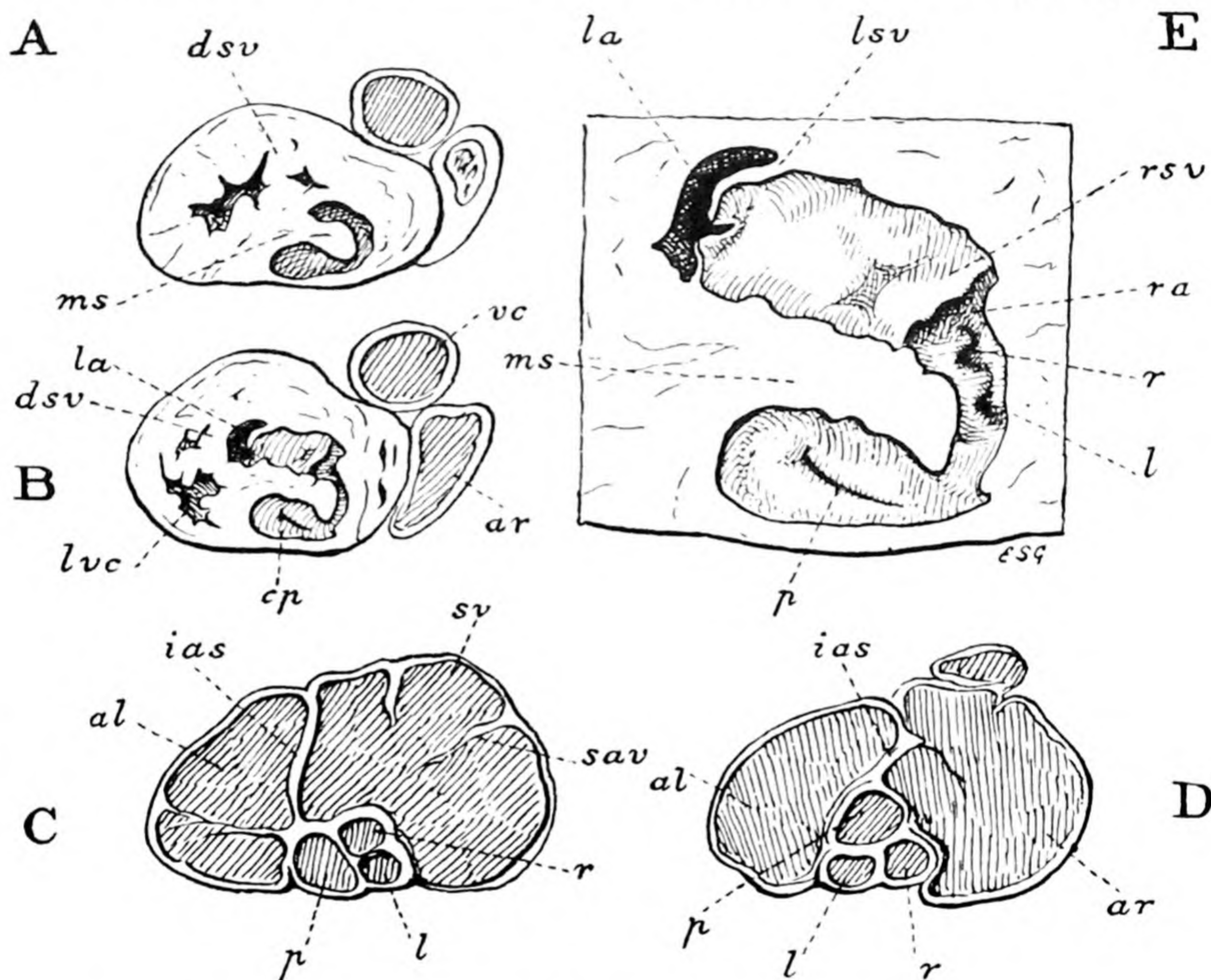
FIG. 569.

Python molurus. Successive transverse sections through heart, seen from behind. E, Portion of Fig. B on a larger scale. *al*, Left auricle; *ar*, right auricle; *vc*, vena cava inferior. Other letters as in Fig. 567.

the ventricular cavity; the opening is thus subdivided into separate right and left auriculo-ventricular apertures, Fig. 570. In ontogeny the valves are derived from a posterior (dorsal) and an anterior (ventral) endocardial cushion (doubtless representing the valves of lower forms), which meet and fuse along the free edge of the septum. Into the cavity of the ventricle projects in all Reptiles an interventricular septum, complete only in Crocodilia, Fig. 587. Leaving for the present the Crocodilia to be dealt with later (p. 563), the second important new feature we meet in the reptilian heart is this incomplete interventricular muscular septum, essen-

tially median and posterior in origin, and tending to divide the cavity into right and left chambers (cavum venosum and cavum arteriosum respectively). It is formed from ingrowing muscular trabeculae. Posteriorly, towards the apex of the ventricle, the septum is complete and dorsoventral; farther forwards, where it is incomplete, its ventral base of attachment (following the external sulcus interventricularis) shifts to the left and becomes continuous with the inpushing due to the bulbo-auricular groove. Thus anteriorly, where the septum reaches near the base of the arterial trunks, it extends almost horizontally with its free edge to the right and joins the ventral endocardial cushion. In this region the cavum arteriosum opens over the edge of the septum freely into the cavum venosum, which is prolonged forwards and to the left into the ventral cavum pulmonale leading to the opening of the pulmonary trunk (see below). The cavum arteriosum (left ventricular cavity) leads antero-dorsally to the septum towards the opening of the right caroticosystemic trunk, while the opening of the left systemic trunk is situated almost opposite the free edge of the septum. Both auriculo-ventricular apertures are dorsal to the septum. From the left auricular opening a stream of blood passes back into the cavum arteriosum, and from the right auricular opening into the cavum venosum. On contraction of the ventricle the venous blood passes into the pulmonary trunk from the cavum pulmonale, mixed blood into the left systemic trunk, and the purest arterial blood into the right carotico-systemic trunk whose opening is a little farther forward. The position of the opening into the left systemic trunk varies a little in different forms, being nearer the opening of the right trunk in Ophidia, and of the pulmonary trunk in Chelonia; but the general disposition of the three openings is remarkably constant throughout the Reptilia, Figs. 547-70.

For it is one of the most characteristic and important features of the heart of all living Reptilia that the cavity of the bulbus cordis becomes subdivided into three separate channels (p. 525), Fig. 571 B. Not only does the main septum pulmo-aorticum grow back to close off the pulmonary trunk (as in all Amniotes), but the remaining trunk is also subdivided by a longitudinal spiral aortic septum into two aortic trunks: one, the carotico-systemic trunk, coming from the left side of the ventricle passes to the right, gives off the carotid arteries, and continues as the right systemic arch; while the other, coming from the right side of the ventricle, passes over to the left, and is continued as the left systemic arch. A pair of semilunar pocket valves protects the openings of each of the three trunks.

An important point to notice in the arterial system of all Reptilia

(and also of Birds), related to the structure of the heart just described, is that the right and left carotid arches come off from the same trunk as the right systemic arch, that is, from the trunk which receives the purest blood from the left side of the ventricle.[1]

The way in which the lumen of the truncus and bulbus cordis becomes subdivided during ontogeny in Reptiles and Birds must now be explained (Langer, 841-2 ; Hochstetter, 836 ; Greil, 831 ; Kerr, 840).   As in Dipnoi
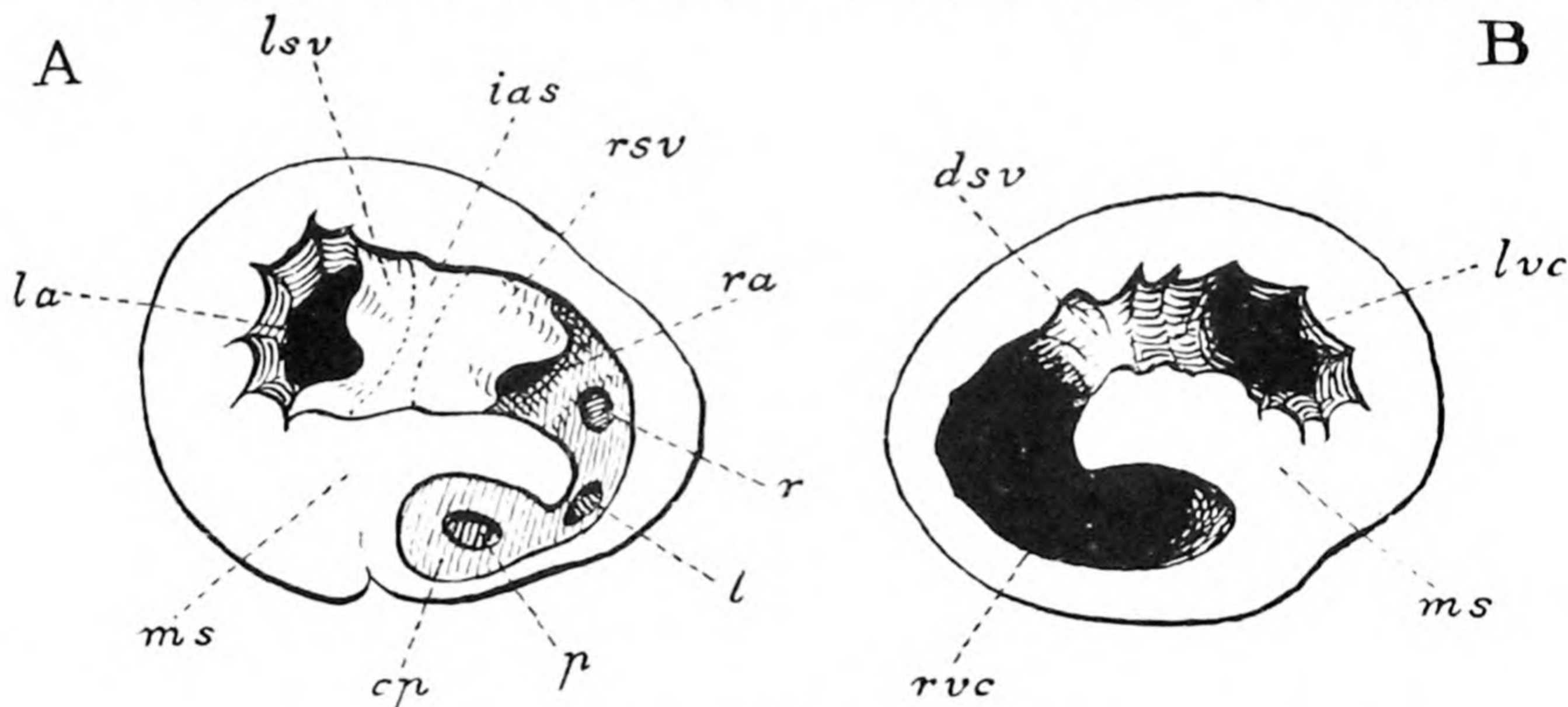
FIG. 570.

Diagrams of ventricle of *Reptilian heart* (not Crocodilian).   A, Cut transversely and seen from behind ; position of interauricular septum is indicated by dotted lines.   B, Cut transversely and seen from in front.   Lettering as in Fig. 567.

and Amphibia, the lumen of the truncus becomes divided into dorsal pulmonary and ventral carotico-systemic channels by the backward growth of the wall between the bases of the fourth and sixth primary arches, Fig. 571.   This horizontal septum joins the anterior ends of the right and left anterior endocardial ridges of the bulbus.   Four such ridges develop in the anterior region of the spirally twisted bulbus cordis, and two approximately dorsal and ventral ridges in the posterior region.[2]   The right anterior ridge is the largest and fuses across with the left, thus

[1] The roots or base of the subclavian arteries to the fore-limbs arise from a pair of segmental arteries, and primitively branch off from the dorsal aorta. Owing to the secondary extension backwards of the bifurcation of the two aortic stems, the subclavians may, as in Lizards, arise from the right aortic arch.   A significant fact is that in Chelonia, Crocodilia, and Aves these primary subclavians are replaced in ontogeny by secondary subclavian arteries coming from the carotid arches, and whose roots have arisen from more anterior segmental arteries.

[2] It will be understood (see pp. 538, 550) that these longitudinal ridges represent originally continuous ridges or rows of valves, extending along the whole bulbar region, and perhaps even as ridges into the ventricle.

continuing backwards the subdivision into pulmonary and carotico-systemic channels; and this aortico-pulmonary septum is completed spirally behind by the junction of the right anterior bulbar ridge with
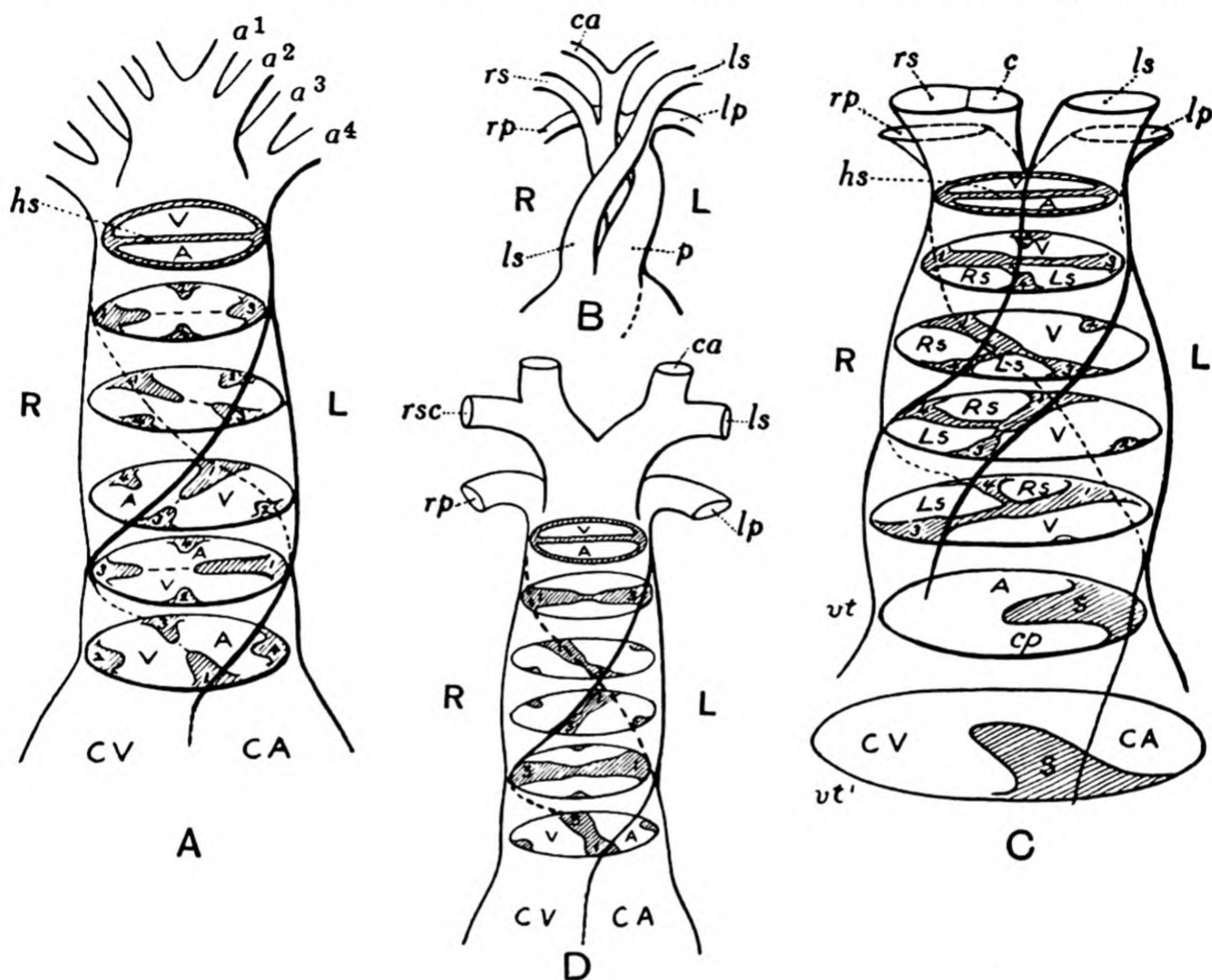
FIG. 571.

Diagrams illustrating the spiral subdivision of *Bulbus cordis* in Dipnoi, Amphibia, Reptilia, Aves, and Mammalia : ventral view ; transverse sections drawn at successive levels showing disposition of endocardial ridges and septa derived from them ; spiral lines indicate their attachment to wall along which tube becomes subdivided in higher forms (solid lines ventrally become broken lines when passing dorsally to bulbus). A, Primitive disposition of ridges in embryo Amniote and retained in adult Dipnoan and Amphibian ; B, oblique view of three trunks formed in Reptile ; C, ridges and septa in Reptile (in Bird ridges 3 and 4 come together and obliterate *Ls*) ; D, Mammal. Most anterior section shows *A*, arterial, and *V*, venous channels separated by horizontal septum, *hs*, in truncus ; *A* leads to left side of ventricle (*CA*, cavum arteriosum), *V* leads to right side (*CV*, cavum venosum). 1, 2, 3, 4, endocardial ridges of spiral bulbus (conus) ; a^{1-4}, adult arterial arches, venous channel leads to $a^{3, 4}$, arterial channel to $a^{1, 2}$; *c*, carotid trunk ; *ca*, carotid arch (a^1) ; *cp*, cavum pulmonale ; *p*, *rp*, left and right pulmonary arch (a^4) ; *ls*, *Ls*, left, *rs*, *Rs*, right systemic arch (a^2) ; *p*, pulmonary trunk ; *rsc*, right subclavian (base of *rs*) ; *S*, interventricular septum ; *vt* and vt^1, sections across anterior end of ventricle.

the ventral posterior and the left anterior ridge with the dorsal posterior, these two posterior ridges also fusing across.[1] The pulmonary channel now opens into the ventricle (cavum pulmonale) ventrally towards the

[1] The two posterior ridges are doubtless the hinder portions of the right and left anterior ridges, the originally continuous ridges having been interrupted (see p. 550).

right, and the carotico-systemic opens into the ventricle more dorsally. The further subdivision of the carotico-systemic channel in Reptiles into left systemic (opening to the right) and right carotico-systemic (opening to the left) is brought about by the formation and backward extension of a septum aorticum derived from the right and ventral endocardial
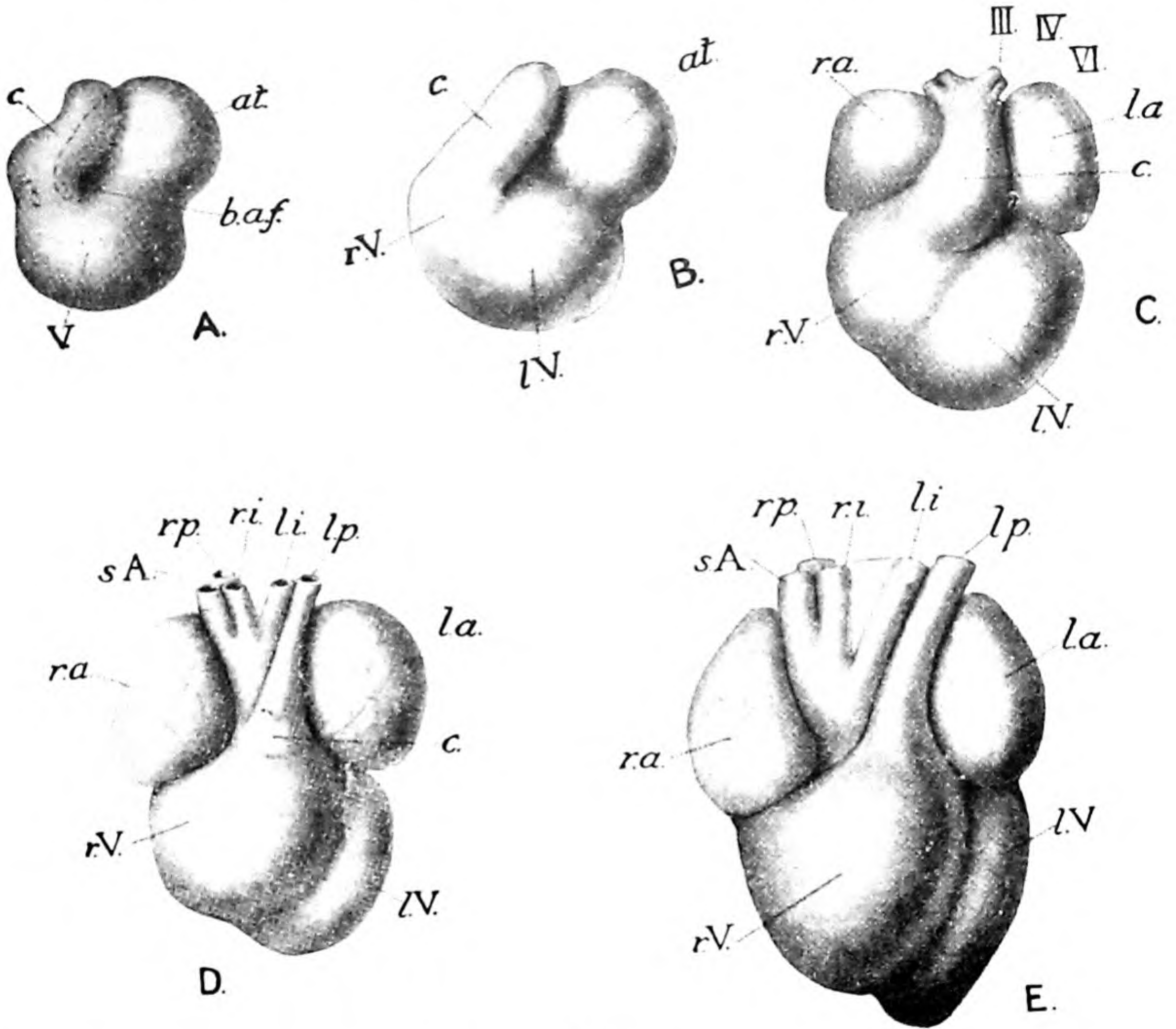
FIG. 572.

Illustrating the development of the heart in the fowl. (After original drawings by Greil.) *at*, Atrium; *b.a.f*, bulbo-auricular fold; *c*, conus; *l.a*, left auricle; *l.i*, left innominate artery; *l.p*, left pulmonary; *l.V*, left ventricle; *r.a*, right auricle; *r.i*, right innominate artery; *r.p*, right pulmonary; *r.V*, right ventricle; *s.A*, systemic aorta. (From Kerr, *Embryology*, 1919.)

ridges of the bulbus. The pairs of pocket valves at the base of each of these three channels are derived from the posterior ridges.

In Birds (Langer, 842; Takahashi, 874) the anterior left and ventral ridges appear to have combined, and no subdivision of the carotico-systemic channel at the base of the trunk occurs, since the left systemic arch is obliterated before these septa are completed. Thus although the two systemic arches are present in early stages, the Bird, so far as known, does not normally pass through a Crocodilian stage with the left opening

independently into the ventricle (this may occur occasionally as an abnormality [Bremer]).

The formation of the longitudinal septa from the bulbar ridges in Dipnoi and Tetrapoda is explained in the diagrams here given, Figs. 563, 571. Whether their spiral course is due to the actual twisting of the heart or merely to their kinking and spiral growth is doubtful; but if the bulbus cordis is twisted to the right the more posterior region must be twisted to the left, since the two extremities are fixed (Kerr, 840).
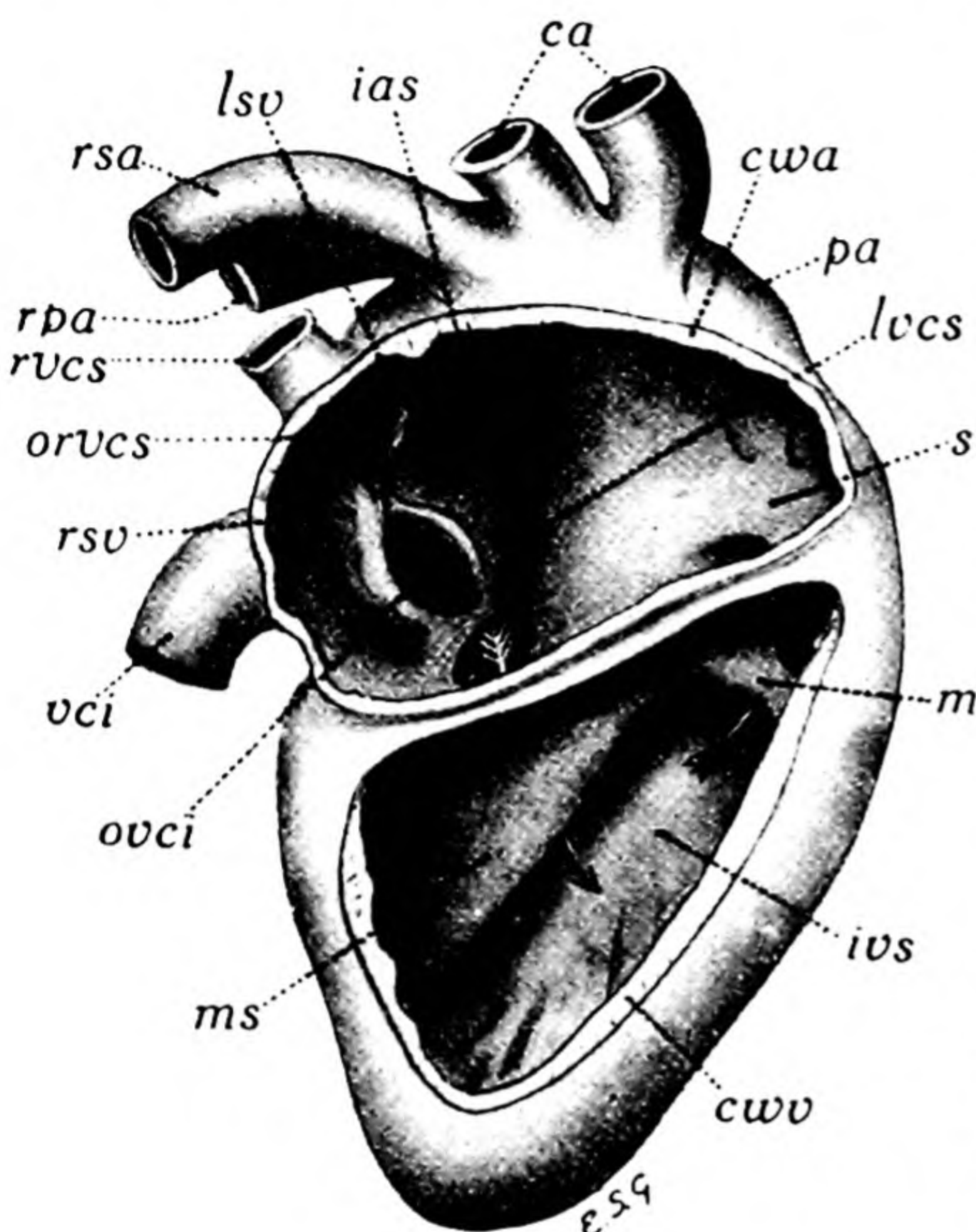
FIG. 573.

Heart of Swan, *Cygnus olor*; seen from right side, and opened so as to expose cavity of right auricle and of right ventricle (an arrow passes through auriculo-ventricular opening). *ca*, Carotid arches; *cwa*, cut wall of right auricle; *cwv*, cut wall of right ventricle; *ias*, interauricular septum; *ivs*, interventricular septum; *lsv*, left sinu-auricular valve; *lvcs*, opening of left vena cava superior; *m*, muscular band; *ms*, muscular portion of auriculo-ventricular valve; *orvcs*, opening of right vena cava superior; *ovci*, opening of vena cava inferior; *pa*, base of pulmonary arch; *rpa*, right pulmonary arch; *rsa*, right systemic arch; *rsv*, right sinu-auricular valve; *rvcs*, right vena cava superior; *s*, septal portion of auriculo-ventricular valve; *vci*, vena cava inferior. An arrow passes under *m* into base of pulmonary trunk.

In the majority of modern Reptilia, the attempt, so to speak, to separate the arterial from the venous stream is only partially carried out in the heart itself, and in the peripheral arteries mixed blood is again brought into the circulation by the opening of the left systemic arch into the dorsal aorta. Along the Sauropsidan phyletic line only the Birds have succeeded in completely separating the two streams. For in these warm-blooded Amniotes not only is the arterial blood of the left ventricle completely shut off from the venous blood of the right ventricle by the completion of the interventricular septum, but the now useless, or actually harmful, left systemic arch is entirely suppressed, Figs. 572-3.

In the avian heart the sinus venosus is so much reduced and subdivided that the great veins appear to open separately into the right auricle (Röse, 862; Kern, 839). The two sinu-auricular valves may be much modified. The pulmonary veins may also open separately into the left auricle. The ventricles become very unequally developed, the wall of

the left being thicker and more muscular than that of the right which partially surrounds it. The left auriculo-ventricular aperture is provided with membranous valves surrounding it (usually an outer and an inner or septal valve). The valve guarding the right auriculo-ventricular aperture is very characteristic. Instead of the membranous valve attached to the interauricular septum found in Reptiles, there is in Birds a large, almost entirely muscular valve attached round the ventral edge of the aperture and to the outer wall of the right ventricle, and stretching far into the ventricular cavity; it appears to be almost entirely developed from the ventricular muscle, and is held ventrally by a stout muscular bridge to the outer wall; the reptilian 'septal' valve seems to be represented by at most a membranous vestige passing round to the inner or medial wall of the ventricle. The only trunk issuing from the right ventricle is the pulmonary, whose opening is provided with three semilunar valves. The only trunk issuing from the left ventricle is the carotico-systemic, also having three semilunar valves at its base; this trunk passes dorsally to the right over the pulmonary, and splits into the carotid arteries and right systemic arch. Thus in the adult Bird the pulmonary and systemic circulations are completely separated, Figs. 573-9. The resemblances of the 'four-chambered' avian heart to that of the mammal are superficial and misleading, and the clue to its structure and origin must be sought in the crocodilian heart (Beddard and Mitchell, 808; Greil, 831; Goodrich, 517, 826). For in the Crocodilia also the interventricular septum has been completed to separate the cavity of a left ventricle with powerful muscular walls from that of a weaker right ventricle, in such a way that the pulmonary and left systemic trunks receive all the venous blood and the right carotico-systemic trunk all the arterial blood. As in other Reptiles the aortic trunks cross at their base, and the interventricular septum is finally completed by fusing with the wall formed between them; so that the right trunk opens into the left cavity, and the left trunk together with the pulmonary into the right cavity. A comparison of the avian and crocodilian hearts shows that they are built on the same plan, agree in almost every detail, except that the crocodilian is more primitive and preserves the left systemic arch and trunk. Near the base of the systemic trunks, just anterior to the semilunar valves, there is in the Crocodilia a small foramen (foramen of Panizza) allowing blood to pass from one arch to the other, and perhaps serving to equalise the pressure within them.[1] The muscular valve, at the right auriculo-

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[1] According to Greil this is a secondary perforation formed late in development. It would seem more probable, however, that it is a remnant of the original communication.

ventricular aperture, so characteristic of Birds, is already developed in Crocodilia, which also preserve a considerable portion of the membranous septal valve, Figs. 580-82, 587.

Exactly how the interventricular septum becomes completed in Birds has been studied by Lindes (1865), Masius (847), Hochstetter (835), Lillie (845), and more recently by Takahashi (874). In the embryonic heart, by the time the endocardial cushions have fused to divide the right from the left auriculo-ventricular apertures,

FIG. 574.

Transverse section through the ventricles of *Grus cinerea*. *S*, septum ventriculorum; *Vd*, right, and *Vg*, left ventricle.

the interventricular septum has reached the dorsal cushion above and the ventral cushion below; but the cavum arteriosum still freely communicates in front of the free edge of the septum with the cavum venosum on the right. This portion of the ventricular cavity now appears as a narrow passage running in a groove below the united cushions, Fig. 577. The interventricular septum next grows on to the endocardial rudiment of the right septal valve, and joining the septum aorticum of the bulbus finally closes the communication completing the wall between the arterial and venous streams, Fig. 578. The morphology of this wall is better understood by studying its development in the Crocodilia. Here the right septal valve is well developed, and its free membranous edge remains in the adult projecting into the right ventricle attached to the interventricular septum, Fig. 582; its base, however, is involved in the completion of the septum from the arterial channel takes place

FIG. 575.

Reconstruction of heart of chick embryo of 5·7 mm. head-length, seen from right side. Part of wall of right auricle is cut away. (After Masius, from F. R. Lillie, *Devel. Chick.* 1919.) *B.Co*, Bulbus cordis; *D.C*, duct of Cuvier; *E.C.d*, *v*, dorsal and ventral endothelial cushions; *O.S.v*, opening of sinus venosus into right auricle; *O.1*, passage below interauricular septum; *O.2*, secondary ostia in interauricular septum.

septum. The closing of the venous by the centripetal growth inwards of the edge of the interventricular septum from behind and above, the septum aorticum (between the right

and left systemic trunks) from in front, and the endocardial rudiment of the right septal valve, which all combine to complete the spiral partition, Figs. 580-81. The more or less complete disappearance of the right septal valve in Birds is probably related to its sharing in the formation of this partition.

The history of these a t r i o - v e n t r i c u l a r v a l v e s may be briefly given as follows. In the Amphibia the dorsal and ventral endocardial cushions spread round the single atrio-ventricular aperture and give rise to two main dorsal and ventral valves, and two smaller right and left valves,
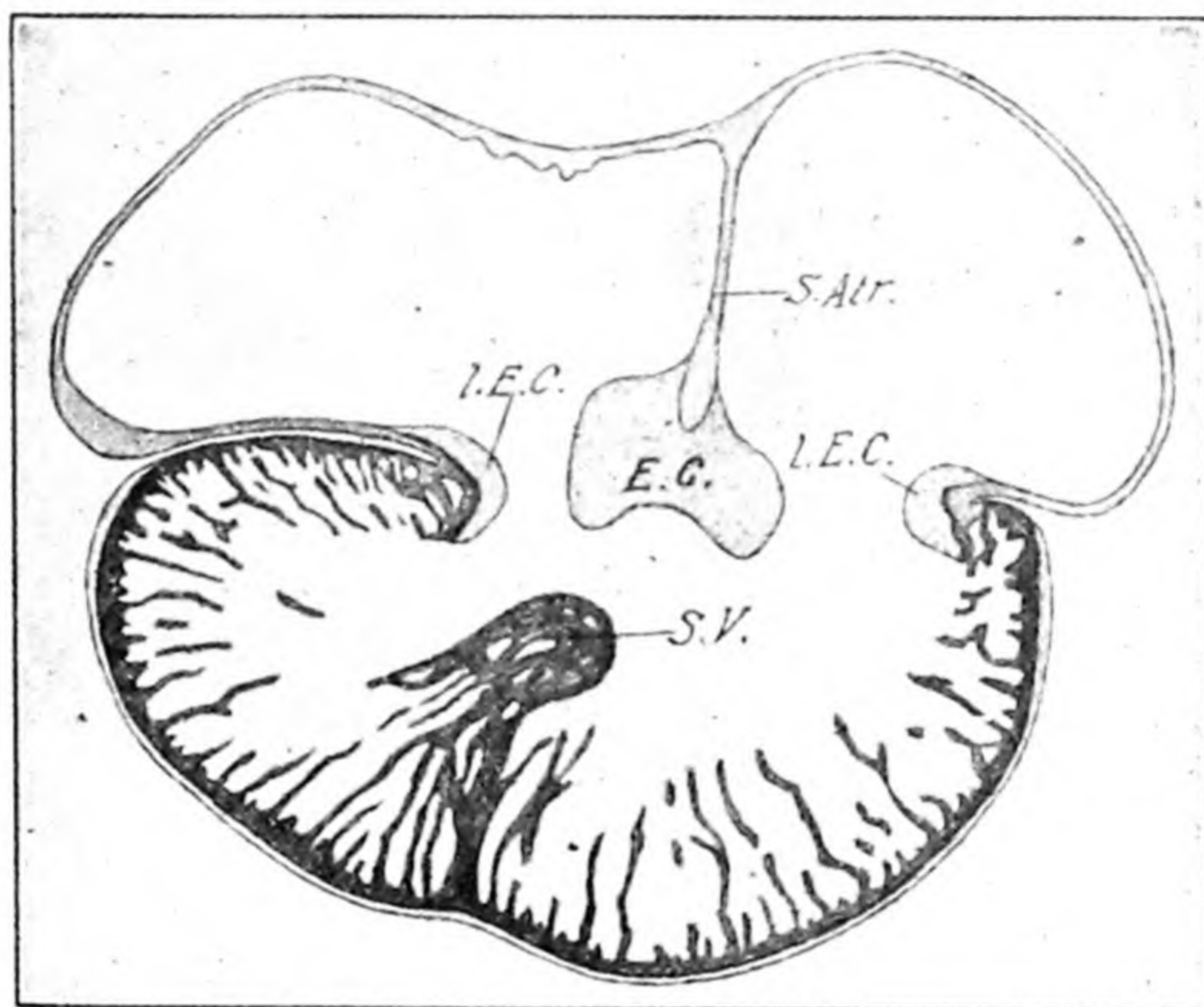
Fig. 576.

Frontal section of heart of chick embryo of 9 mm. head-length. After Hochstetter (from F. R. Lillie, *Develt. Chick*, 1919). *E.C*, Median endothelial cushion ; *l.E.C*, lateral endothelial cushion ; *S.Atr*, septum altriorum ; *S.V*, septum ventriculorum.

Fig. 558. In the Amniota the cushions meet and fuse across with each other and the free edge of the interauricular septum, thus dividing the aperture into right (venous) and left (arterial) openings. The dorso-ventral endocardial ridge thus formed gives rise to a ' septal ' valve on either side in all Reptilia, Fig. 570. But in the Crocodilia, although similar septal valves are developed, the endocardial cushion on the left also spreads round the auriculo-ventricular aperture and forms an opposing valve attached to the outer wall of the left ventricle ; while at the right auriculo-ventricular opening the right septal valve is supplemented by a muscular valve from the outer wall of the ventricle. The atrio-ventricular valves of Birds resemble those of Crocodiles, but are more specialised.

The Mammalia also have succeeded in separating the venous from the arterial circulation, but in a different way. In the mammalian heart

the sinus is more completely suppressed than in other Amniotes,[1] its remains being incorporated in development into the wall of the right
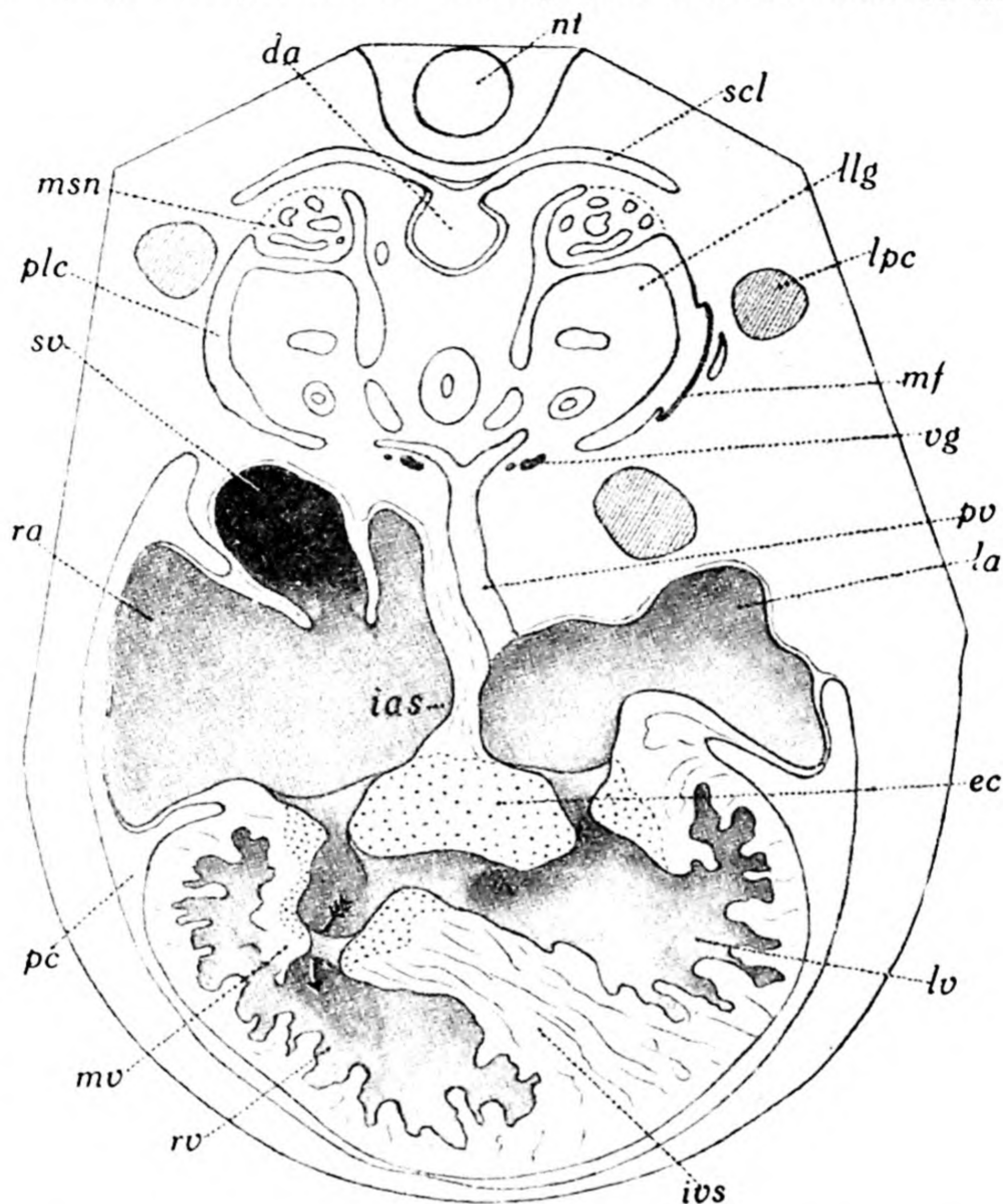
FIG. 576a.

Transverse section of trunk of embryo duck of 7 days, *Anas platyrhyncha*, showing heart cut through auriculo-ventricular openings and seen from in front. *da*, Dorsal aorta; *ec*, endocardial cushion, and *ivs*, incomplete interventricular septum, with interventricular passage still widely open between; *la*, *ra*, left and right auricles; *llg*, left lung; *lpc*, left cardinal vein; *lv*, *rv*, left and right ventricles; *mf*, lip of Müllerian funnel; *msn*, mesonephros; *mv*, muscular valve attached by strand to septum (arrow passes behind); *nt*, notochord; *pc*, pericardial cavity; *plc*, pleural cavity; *pv*, pulmonary vein; *scl*, primitive subclavian; *sv*, sinus venosus; *vg*, branch of vagus.

auricle, and the three great veins coming to open directly into the auricular cavity. The sinu-auricular valves, still fairly well shown in the Monotremata, are much reduced and modified in Ditremata. On the dorsal

[1] This suppression of the no longer necessary sinus venosus seems to have occurred to some extent independently in various groups, and the relative position of the venous apertures, as well as the modification of the valves, varies much in different forms (Röse). That portion of the auricular wall derived from the sinus is smoother and less muscular than the rest.

wall of the auricle opens the right vena cava superior, near the middle the vena cava inferior, and more posteriorly and to the left the left
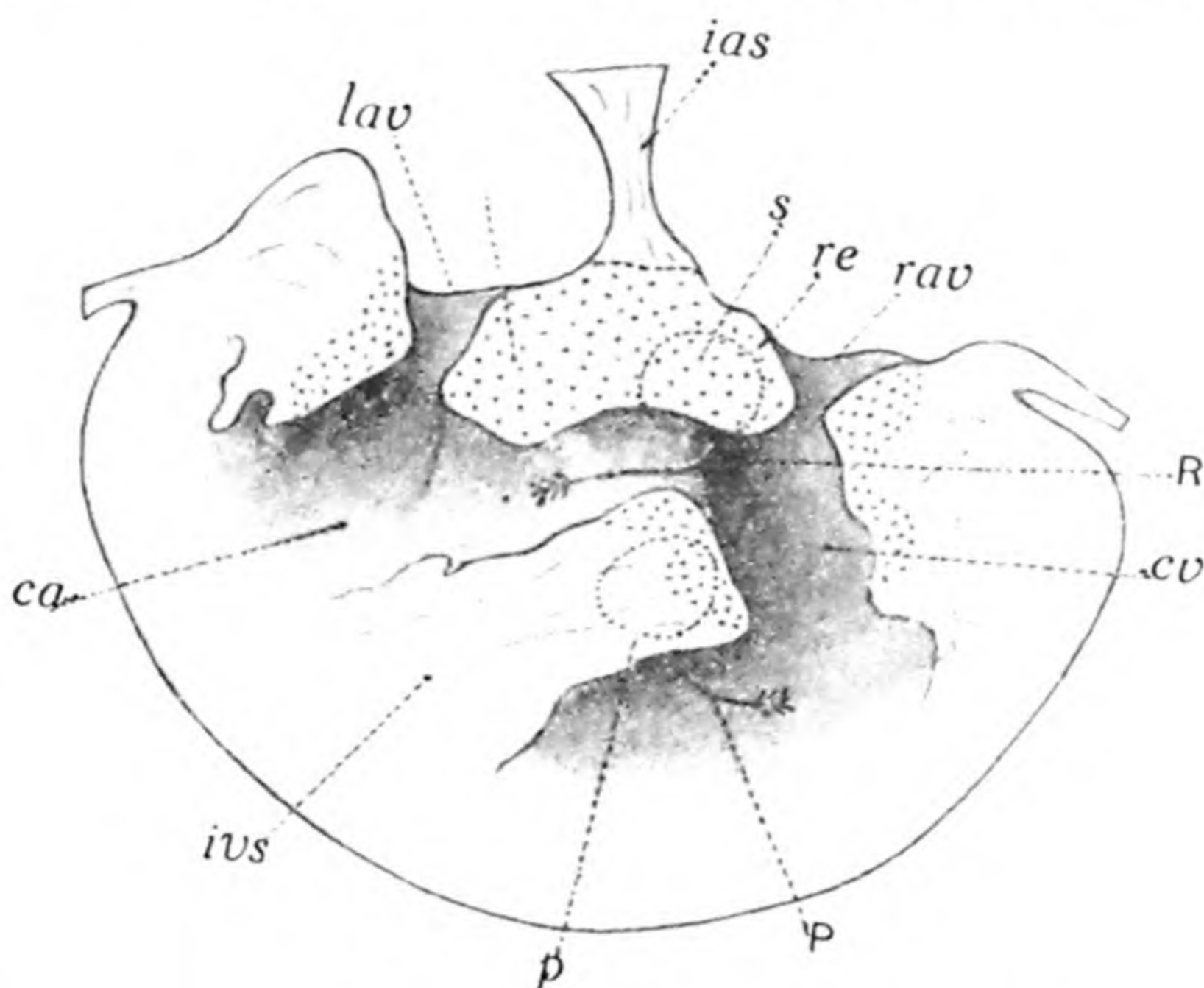
FIG. 577.

Embryo duck, *Anas* : Posterior portion of ventricles of heart shown in Fig. 576 seen from behind. Upper arrow passes into base of right systemic trunk, *R* ; lower arrow into base of pulmonary trunk, *P*. *ca*, *cv*, Cavum arteriosum and cavum venosum ; *lav*, *rav*, left and right auriculo-ventricular openings ; *le*, *re*, left and right endocardial rudiments of septal valves ; *p*, dotted line shows position farther forward of pulmonary opening, and *s* position of systemic opening. Interventricular passage still widely open.
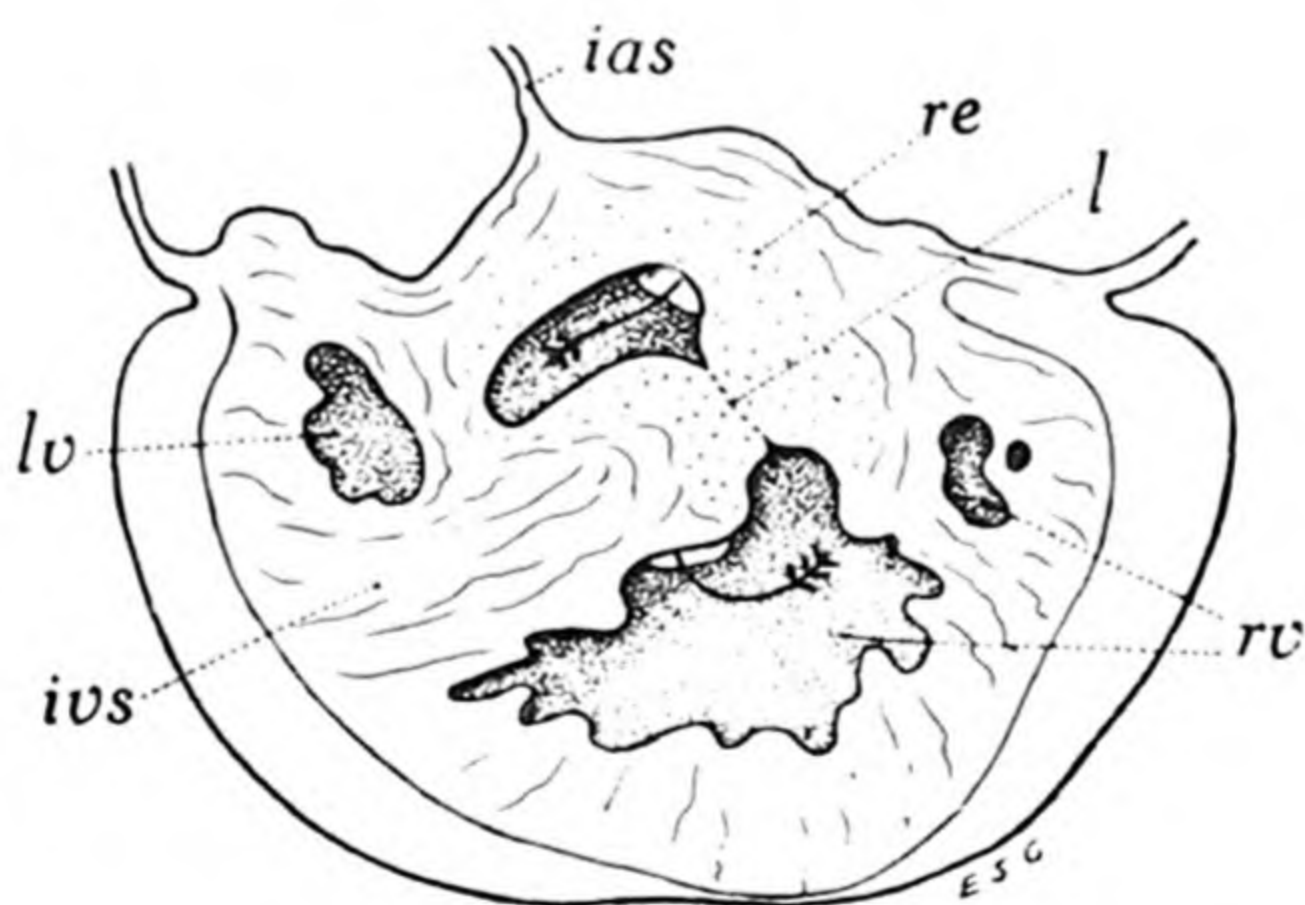
FIG. 578.

Ventricles of heart of *Passer* shown in Fig. 579, cut farther forward. Vestige of closure of interventricular passage at dotted line, *l*. Upper arrow into base of right systemic trunk, lower arrow into pulmonary trunk. Other letters as in Fig. 579. (Partly from wax model made by G. R. de Beer.)

v. c. superior.[1] The right sinu-auricular valve extends along the right edge of the openings, and remains as a rule in the adult as a Eustachian valve protecting the opening of the v. c. inferior, and Thebesian

[1] In many mammals (Edentate, Carnivora, Primates) the left vena cava superior disappears after the formation of anastomosis carrying the venous blood from the left side into the right v. c. superior.

valve protecting the openings of the left v..c. sup. and coronary sinus.
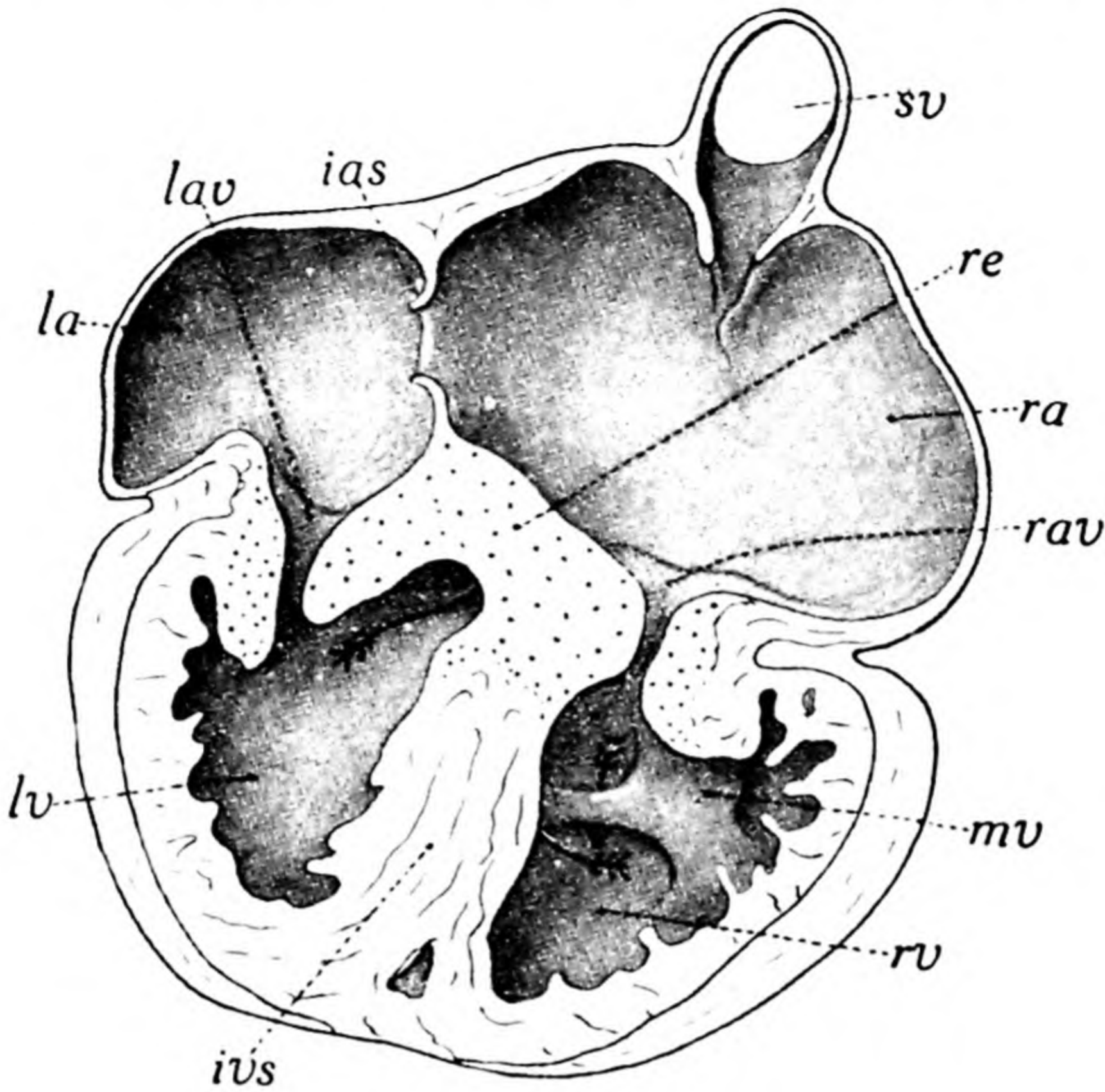
FIG. 579.

Heart of embryo *Passer domesticus*, cut transversely through auriculo-ventricular openings, *lav*, *rav*, at stage immediately after completion of interventricular septum, *ivs*; seen from behind (cp. Fig. 577). *ias*, Interauricular septum (pierced); *mv*, right muscular valve. Other letters as in previous figures. (Partly from wax model by G. R. de Beer.)
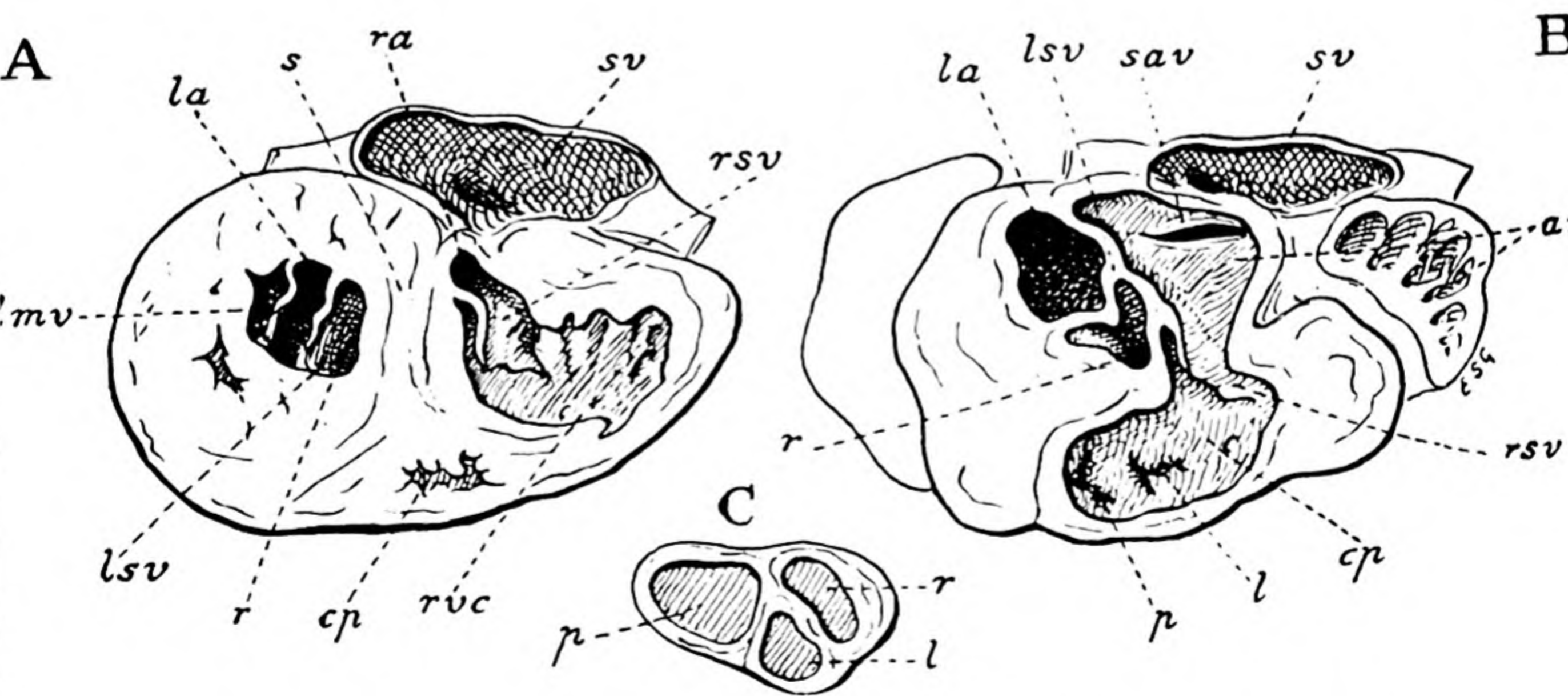
FIG. 580.

Caiman sclerops. Successive transverse sections through the heart, seen from behind: A, Most posterior; C, most anterior. *s*, Interventricular septum; *sv*, sinus venosus; *sav*, sinu-auricular valve. Other letters as in Figs. 568-9.

The pulmonary veins come to open separately into the left auricle, owing to the absorption of their common stem into its wall, Fig. 583.

In development the first formed interauricular septum fuses with the dorsal and ventral endocardial cushions which join across, dividing the
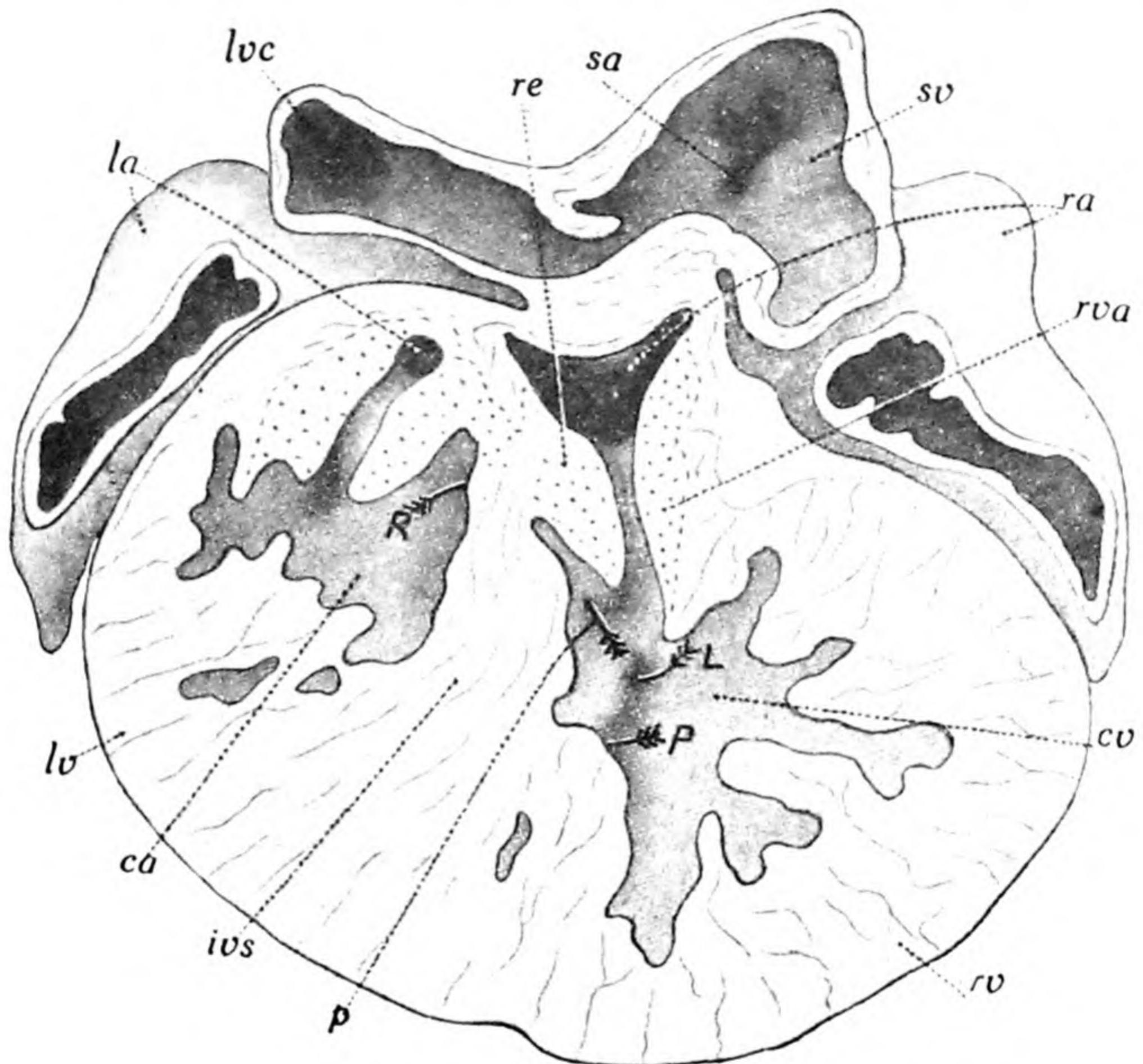
FIG. 581.

Heart of embryo *Crocodilus* sp. cut transversely through auriculo-ventricular openings at stage before completion of interventricular septum; seen from behind. *ca*, Cavum arteriosum, anterior region of left ventricular cavity; *cv*, cavum venosum, anterior region of right ventricular cavity; *ivs*, muscular interventricular septum; *L*, arrow into base of left systemic trunk; *la*, *ra*, left and right auricles (wall partially cut away); *lv*, *rv*, cut wall of left and right ventricles; *lvc*, left vena cava anterior; *P*, arrow into base of pulmonary trunk; *p*, arrow into interventricular passage over free edge of septum; *R*, arrow into base of right systemic trunk; *re*, right septal valve; *rva*, right valve guarding auriculo-ventricular opening; *sa*, sinu-auricular opening; *sv*, sinus venosus. Endocardial cushions dotted.

ventricular aperture into right and left atrio-ventricular openings. This septum becomes perforated (foramen ovale) in the embryo (as in Reptiles and Birds) and is later completed by a second septal fold in combination with the left sinu-auricular valve. The cushions grow round the two openings to form the auricular ventricular valves (three tricuspid valves on the right, and two mitral valves on the left).[1] Meanwhile a longitudinal

[1] The conversion of the thickenings into membranous valves takes place by their being hollowed out into thin folds from the ventricular side leaving muscular cords stretching from the edge to the wall of the ventricle. Later the muscle of the valve and the cords is replaced by connective tissue. In
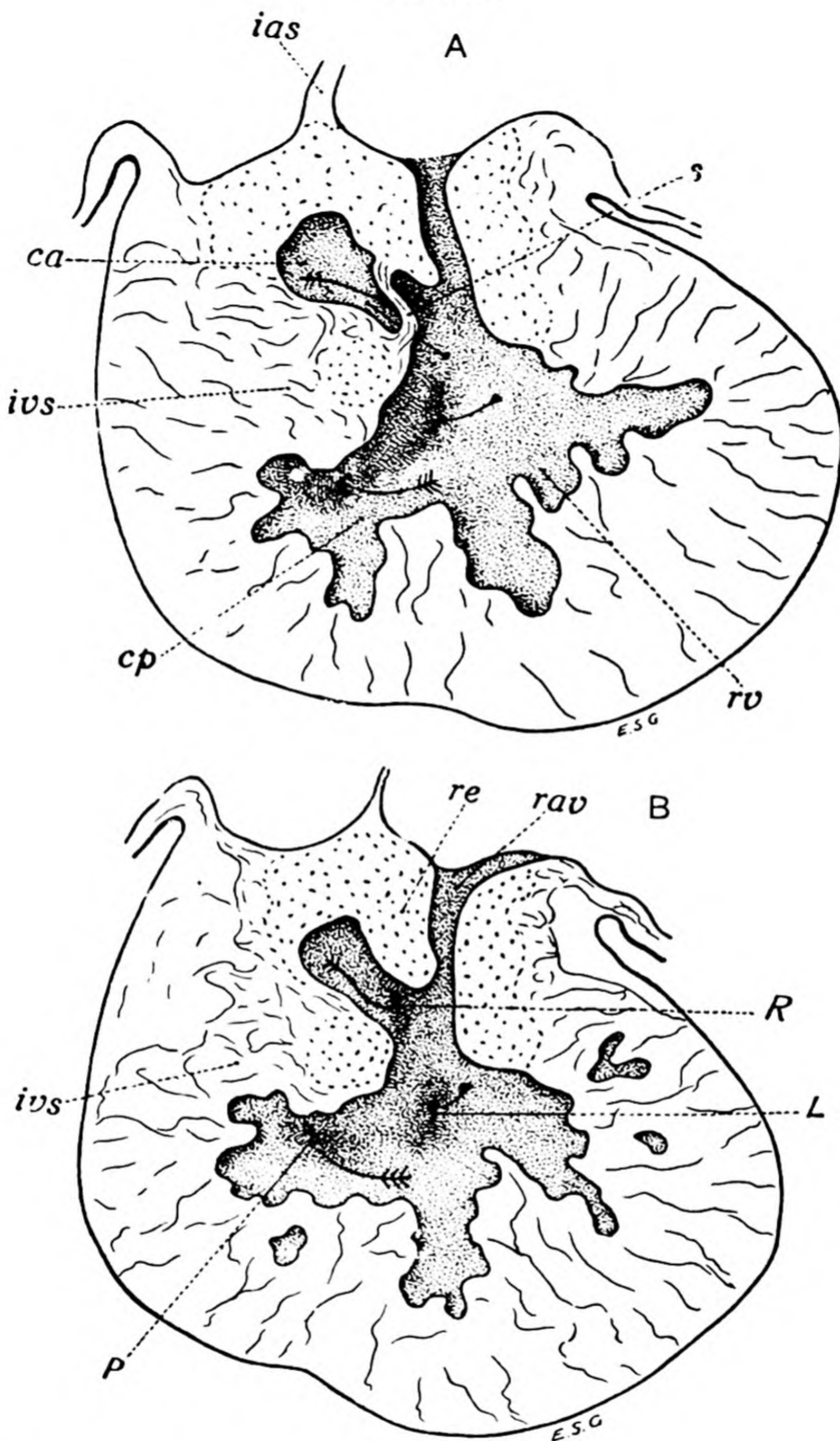
FIG. 582.

Ventricles of heart of *Crocodilus* shown in Fig. 581, cut farther forward in A and still farther forward in B.   A pin is shown in A, through interventricular passage which is fully opened up in B.   *s*, Thin fold which will by growing forward to right finally separate cavum arteriosum from cavum venosum ; *rav*, right auriculo-ventricular opening.   Other letters as in Fig. 581.

the Monotreme Ornithorhynchus, however, a considerable amount of muscle remains in the outer flap of the tricuspid valve, while the inner flaps are small, giving it a certain resemblance to the right valves of a bird (Lankester, 1882–3).

muscular interventricular septum grows forwards from the postero-dorsal wall of the ventricle to meet and fuse with the endocardial cushions between the two auriculo-ventricular apertures. Right and left ventricular cavities are thus formed still communicating with each other in front near the base of the arterial trunks, Figs. 584-5.

As usual in Amniotes, the primitive ventral aorta becomes sub-divided into dorsal pulmonary and ventral aortic (carotico-systemic)
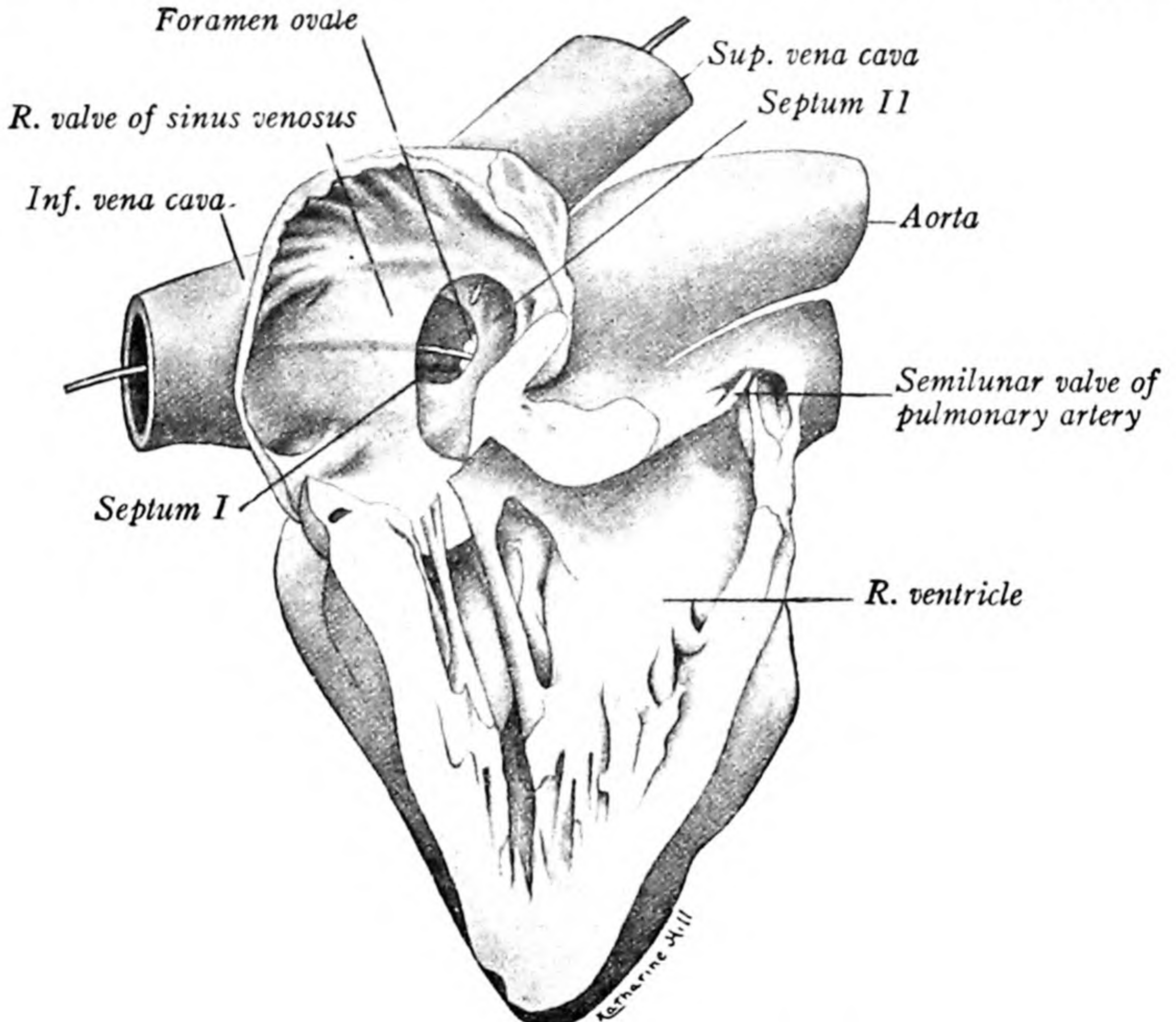
FIG. 583.

Lateral dissection of heart of 65 mm. human foetus viewed from right side. × 12. (From Prentiss and Arey, *Text-book of Embryology*, 1917.)

channels, and this subdivision is carried backwards throughout the bulbus cordis by the formation of a spiral septum due to the fusing across of the right and left endocardial ridges, Figs. 571, 584, 586. At their junction with the ventricle the septum pulmo-aorticum, between the pulmonary trunk on the right and aortic on the left, becomes vertical, and fusing with the edge of the interventricular septum closes the interventricular canal. The right ventricle now leads only to the pulmonary trunk, and the left only to the carotico-systemic trunk. The division of the whole heart into right and left halves is now completed, and the venous

pulmonary circulation separated from the arterial systemic circulation (except for the mixture in the embryo by means of the temporary foramen ovale). It should be noticed that the carotico-systemic vessels are at first symmetrical; from the median trunk come off right and left systemic arches (each giving off a subclavian artery), and right and left carotid arches. Later, while the left systemic or aortic arch remains
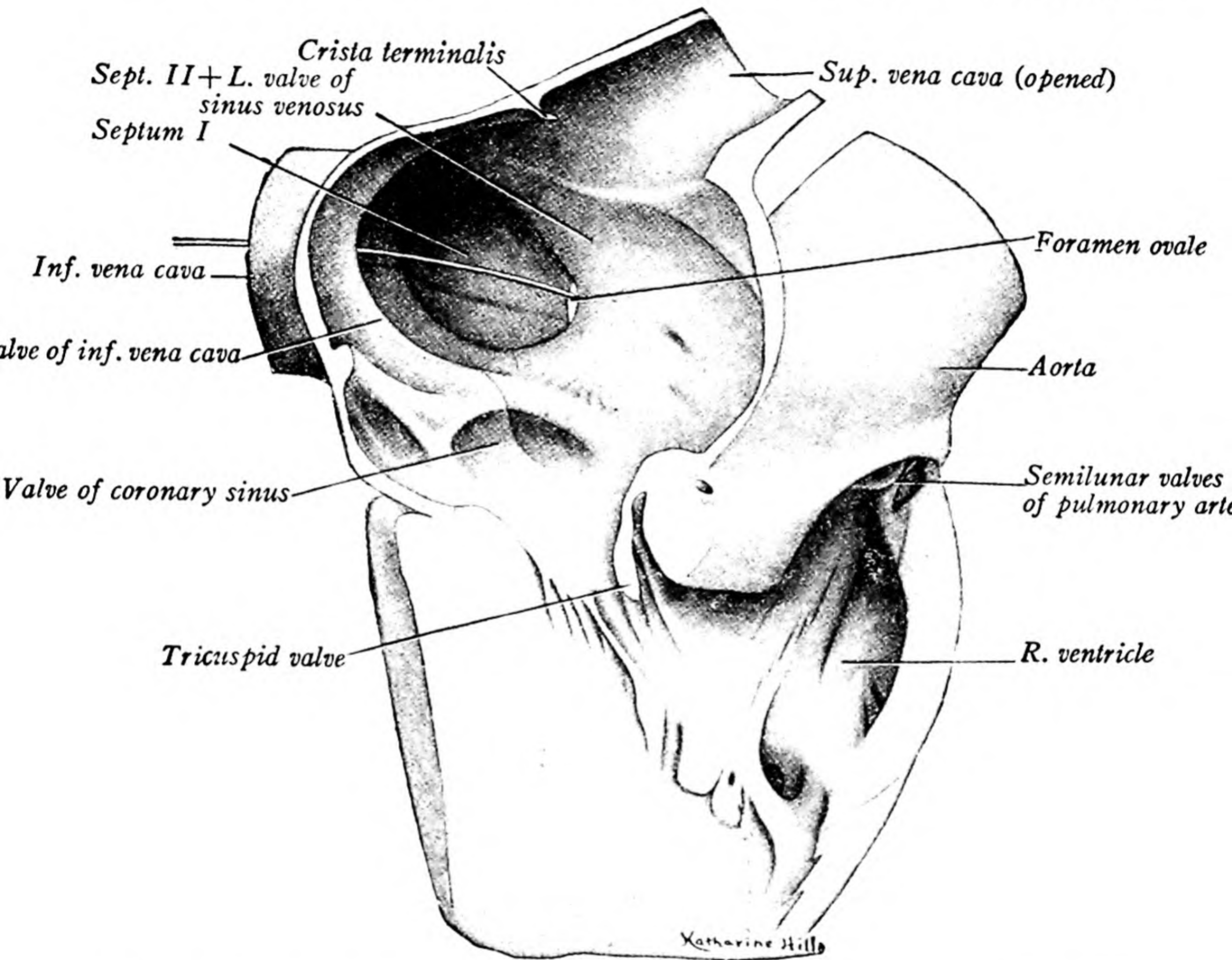
FIG. 583a.

Lateral dissection of heart of 105 mm. human foetus viewed from right side. ×7. (From Prentiss and Arey, *Text-book of Embryology*, 1917.)

complete and passes into the dorsal aorta, the right is interrupted dorsally and posteriorly, ceases to join the aorta, and forms in the adult mammal merely the base of the right subclavian. As usual, the pocket valves protecting the entrance to the pulmonary and aortic trunks are formed from the posterior ends of the endocardial ridges.

The seldom fully appreciated but nevertheless great significance in phylogeny of the structure of the heart may now be pointed out. Since all living Reptiles possess the reptilian type of heart, with its quite char-

acteristic specialisations, they have in all probability been derived from

A

Pulmonary artery —   — Aorta

Incomplete bulbar septum —   Dorsal endocardial cushion

Ventral endocardial cushion —   Atrio-ventricular foramen

Interventricular septum

Interventricular sul

B

Aorta —   Pulmonary artery

Arrow in pulmonary artery —   Base of aorta

Proximal bulbar septum —

Interventricular foramen —   Arrow in aorta

R. atrio-ventricular foramen —   L. atrio-ventricular foramen

R. ventricle —   Interventricular septum

FIG. 584.

Ventral view of stages in development of heart to show differentiation of bulbus cordis into aorta and pulmonary trunk (Kollman) : A, Heart of 5 mm. human embryo ; B, of 7·5 mm. human embryo. (From Prentiss and Arey, *Text-book of Embryology*, 1917.)

a common ancestor in which the reptilian type had been developed. The Birds also no doubt came from that same stock, and branched off not
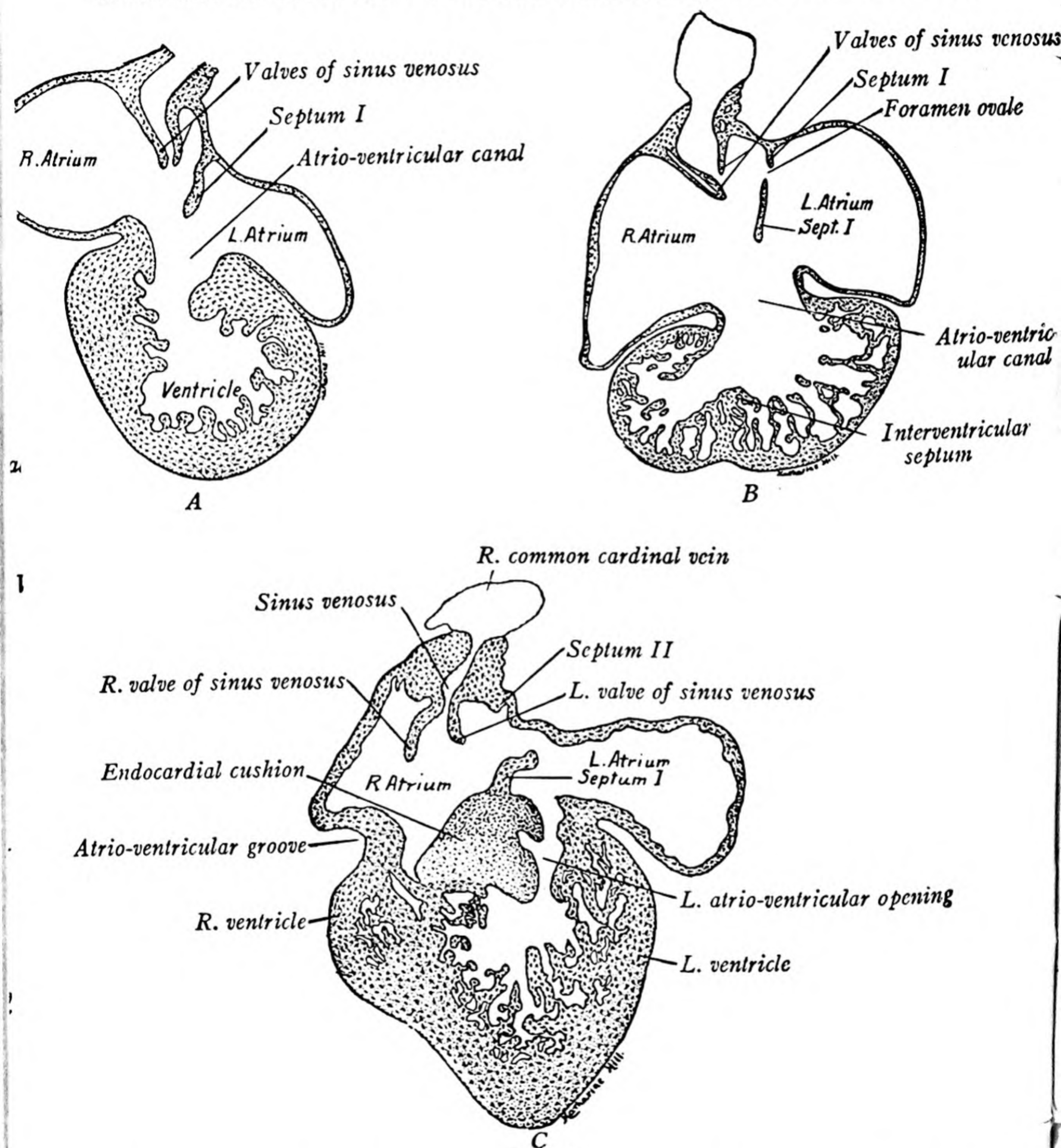
Fig. 585.

Horizontal sections through chambers of human heart : A, 6 mm. ; B, 9 mm. ; C, 12 mm. (A and B are based on figures of Tandler.)   × About 50. (From Prentiss and Arey, *Text-book of Embryology*, 1917.)

far from the Crocodilia. But the Mammalia must have branched off and diverged from a common Amniote ancestor before the Reptilian type of specialisation had begun, since, once committed to this line of

specialisation, the heart must inevitably evolve in the reptilian and crocodilian direction, Fig. 587. Now there is good reason to believe that certain extinct forms (Theromorpha) usually included in the Class Reptilia are, if not the ancestors of the Mammalia, at least closely allied to them. These so-called Reptiles, then, probably possessed a heart of the Mammalian type, or at all events capable of giving rise to this type. It follows that the Class Reptilia, as commonly understood, is an artificial polyphyletic group containing, besides certain primitive Amniotes (Cotylosauria), two distinct diverging branches : one leading to modern Reptilia and eventually also to Birds, and the other leading to Mammalia. These forms may be called the Sauropsidan and Theropsidan Reptiles respectively (Goodrich, 517). While the Reptilia Theropsida are all

Aorta
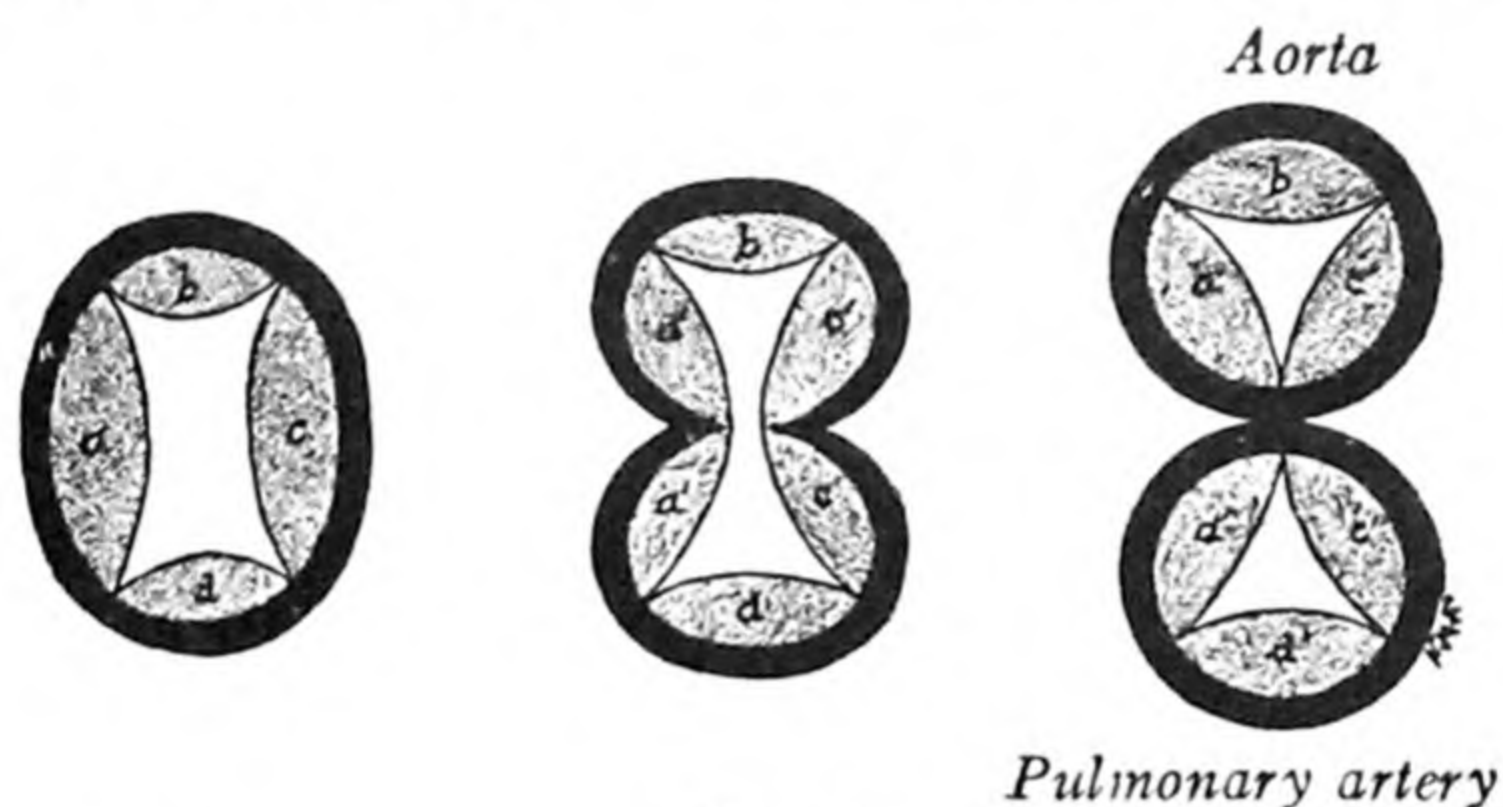
Pulmonary artery

FIG. 586.

Scheme showing division of bulbus cordis and its thickenings into aorta and pulmonary artery with their valves (from Prentiss and Arey, *Text-book of Embryology*, 1917). *a, b, c, d,* Anterior endothelial ridges.

extinct, the Reptilia Sauropsida[1] include all the modern Reptiles and many extinct ones. This conclusion is amply confirmed by evidence derived not only from the skeleton, but also from other parts, such as the lungs, coelomic septa, and brain.

Summary.—We may now briefly recapitulate the probable history of the heart. It developed from the median ventral vessel, immediately behind the gills and in front of the liver, as a muscular enlargement to pump the venous blood through the gills. It became subdivided into chambers (sinus venosus, atrium, ventricle, conus) which contract consecutively from behind forwards, and are separated by valves ensuring the flow of blood forwards. Lodged in the pericardial coelom, the heart acquired an S-shaped bend. From such a primitive condition the heart of Cyclostomes diverged with marked specialisations. In Pisces longitudinal rows of valves developed in the anterior chamber or bulbus cordis, from which is formed the conus.

[1] The term Sauropsida, originally used by Huxley to include all Reptiles as well as Birds, is here used in a restricted sense.
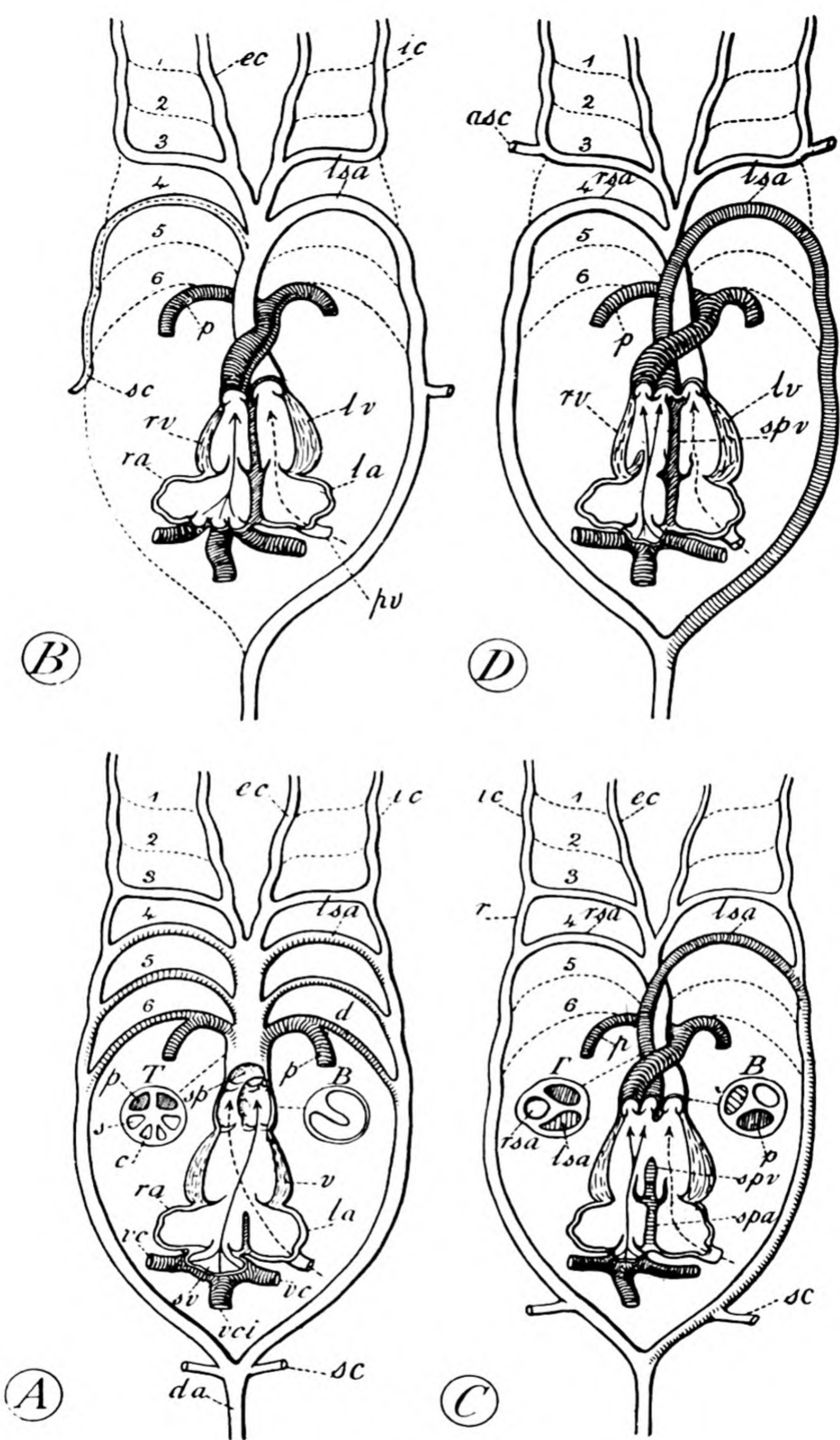
FIG. 587.

Diagrams of *heart* and *aortic arches* in an Amphibian, A; a Mammal, B; a Reptile (Chelonia, Lacertilia, Ophidia, Rhynchocephalia), C; and a Crocodile, D. Ventral view of heart represented as untwisted so as to bring chambers into a single plane, with sinus venosus behind and ventricle in front. B, Transverse section of region of bulbus cordis; T, transverse section of region of truncus arteriosus. *asc*, Anterior subclavian; *d*, ductus Botalli; *ec*, external carotid; *ic*, internal carotid; *la*, left auricle; *lsa*, left systemic arch; *lv*, left ventricle; *p*, pulmonary artery; *r*, portion of lateral aorta remaining open only in *Sphenodon* and some Lacertilia as ductus arteriosus; *ra*, right auricle; *spa*, interauricular septum; *spv*, interventricular septum; *sv*, sinus venosus; *v*, ventricle; *vc*, vena cava superior; *vci*, vena cava inferior. Arrows from sinus venosus indicate main stream of venous blood; arrows with dotted line from left auricles indicate stream of arterial blood. 1-6, Original series of six embryonic aortic arches. (Goodrich, 1916, modified.)

This conus became replaced in the higher Teleostomes by a non-contractile bulbus arteriosus. In Dipnoi and Amphibia the lumen of the heart began to be subdivided longitudinally into right venous and left arterial channels by means of longitudinal ridges and septa ; and the bulbus cordis became spirally twisted. The subdivision was further carried out in the Amniota where the atrio-ventricular opening is divided into two by the junction across of the endocardial cushions and interauricular septum ; the interventricular septum (absent in modern Amphibia) becomes definite, and the lumen of the bulbus cordis is completely divided into pulmonary and carotico-systemic channels. But the further completion of the interventricular septum and separation of the venous and arterial streams was carried out independently along two diverging phyletic lines, the one leading through the Theropsidan Reptiles to Mammalia, and the other through the Sauropsidan Reptiles to Birds.

CHAPTER XI

AIR-BLADDER AND LUNGS

THE AIR-BLADDER OF PISCES

ALL the Tetrapoda being air-breathing vertebrates in the adult condition are provided with lungs : essentially a bilobed outgrowth of the pharynx communicating with it by a median ventral glottis. The only exception to this rule is found in the Urodela, where some species have lost the lungs. Looking for the origin of the lungs in the lower forms, anatomists have long considered them to be represented by the air-bladder of fishes. Owen, having studied the African ' lung-fish ' *Protopterus*, maintained their homology, and it has since been generally adopted. But as it is by no means certain that the various kinds of air-bladder found in fishes are homologous, and since the origin of the bladder itself is not yet fully explained, the whole question remains even at the present time undecided. It is not so simple as appeared at first sight.

Except in certain Teleosts in which it has obviously been lost, some sort of air-bladder exists in all the Osteichthyes, and distinguishes this group from the other and lower fishes in which it is absent. For the suggestion by Miklucho-Maclay that it is represented in Selachians by a small oesophageal diverticulum has not been borne out by later work (Mayer, 850). Perhaps the most primitive air-bladder is seen in *Poly-*

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pterus (Geoffroy Saint-Hilaire, 1825; Kerr, 840), where a bilobed sac, with a short left and a long right lobe, opens on the floor of the pharynx just behind the gill-slits, through a muscular vestibule leading to a glottis slightly to the right of the median line, Figs. 588 B, 592 A. The Dipnoi are provided with a very similar muscular vestibule opening into the oesophagus slightly to the right of the mid-ventral line, and protected by an epiglottis-like fold strengthened by connective tissue (Parker, 854; Göppert, 902). While in *Polypterus* the air-bladder lies ventrally to the oesophagus for the most part, and only the elongated right lobe takes up a position behind in the mesentery dorsal to the gut, in the Dipnoi it lies entirely dorsal to the alimentary canal in the mesentery, between it and the dorsal aorta. It is single in *Ceratodus* but bilobed in *Protopterus* and *Lepidosiren*, and communicates with the vestibule by means of a narrow pneumatic duct passing round the right side of the oesophagus,[1] Figs. 588 C, 591, 592 B.
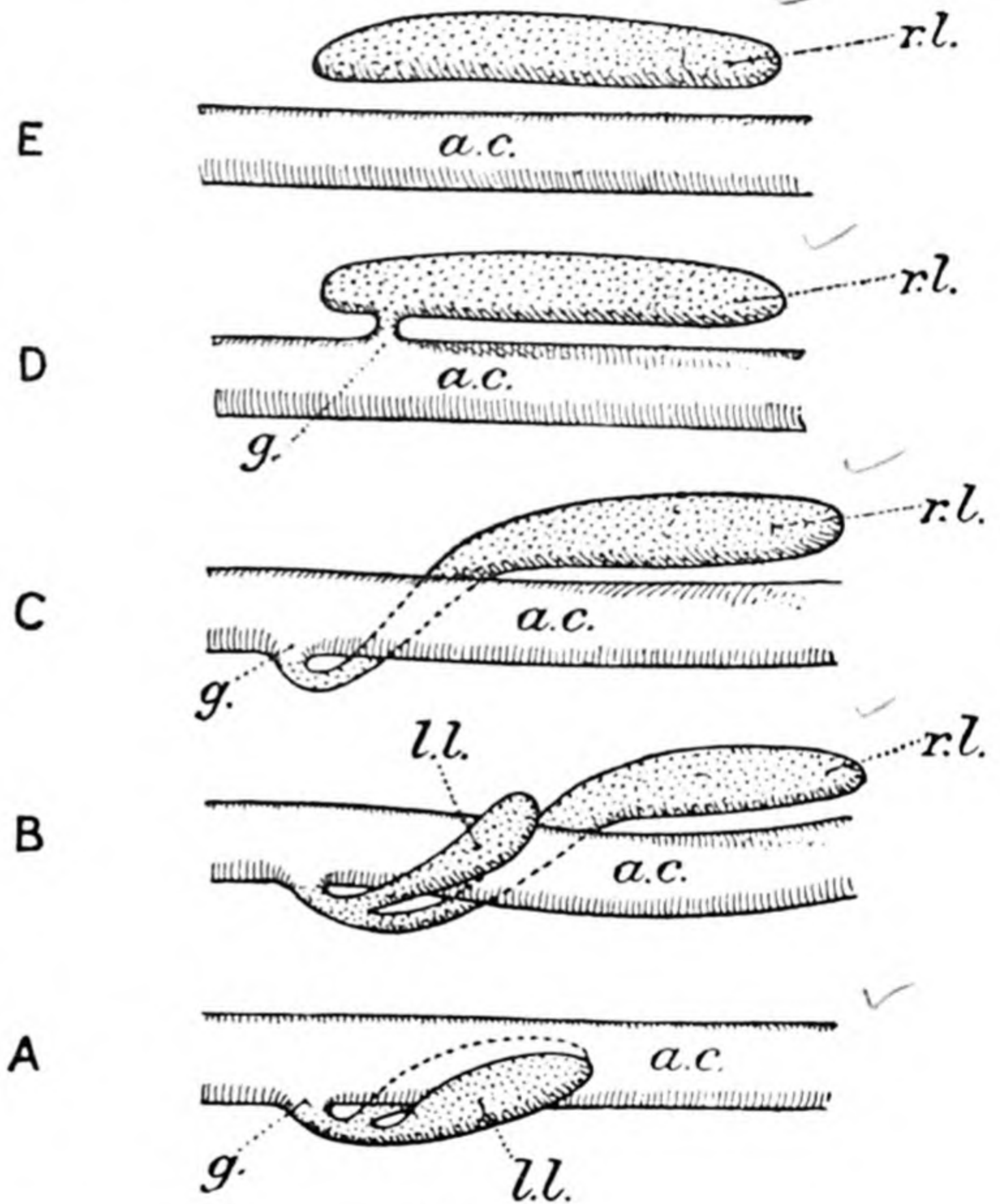
FIG. 588.

Diagram illustrating the lung in fishes; as seen from the left side. A, Primitive symmetrical arrangement; B, *Polypterus*; C, *Ceratodus*; D, physostomous Teleost; E, physoclistic Teleost. *a.c*, Alimentary canal; *g*, glottis; *l.l*, left lung; *r.l*, right lung. (From J. G. Kerr, *Zoology*, 1921.)

In the remainder of the Osteichthyes, that is to say in all the Actinopterygii, the air-bladder is essentially a median dorsal diverticulum of the alimentary canal lying between it and the dorsal aorta, and outside the coelom (retroperitoneal). It usually opens into the oesophagus by a ductus pneumaticus, originally described by Needham in 1667. This

[1] Wiedersheim (946) has suggested that there were originally two larynges: one dorsal and median (*Lepidosteus*), and one ventral and median (Dipnoi and *Polypterus*). But there is little to support this view, partly based on erroneous observations, and it has not been accepted.
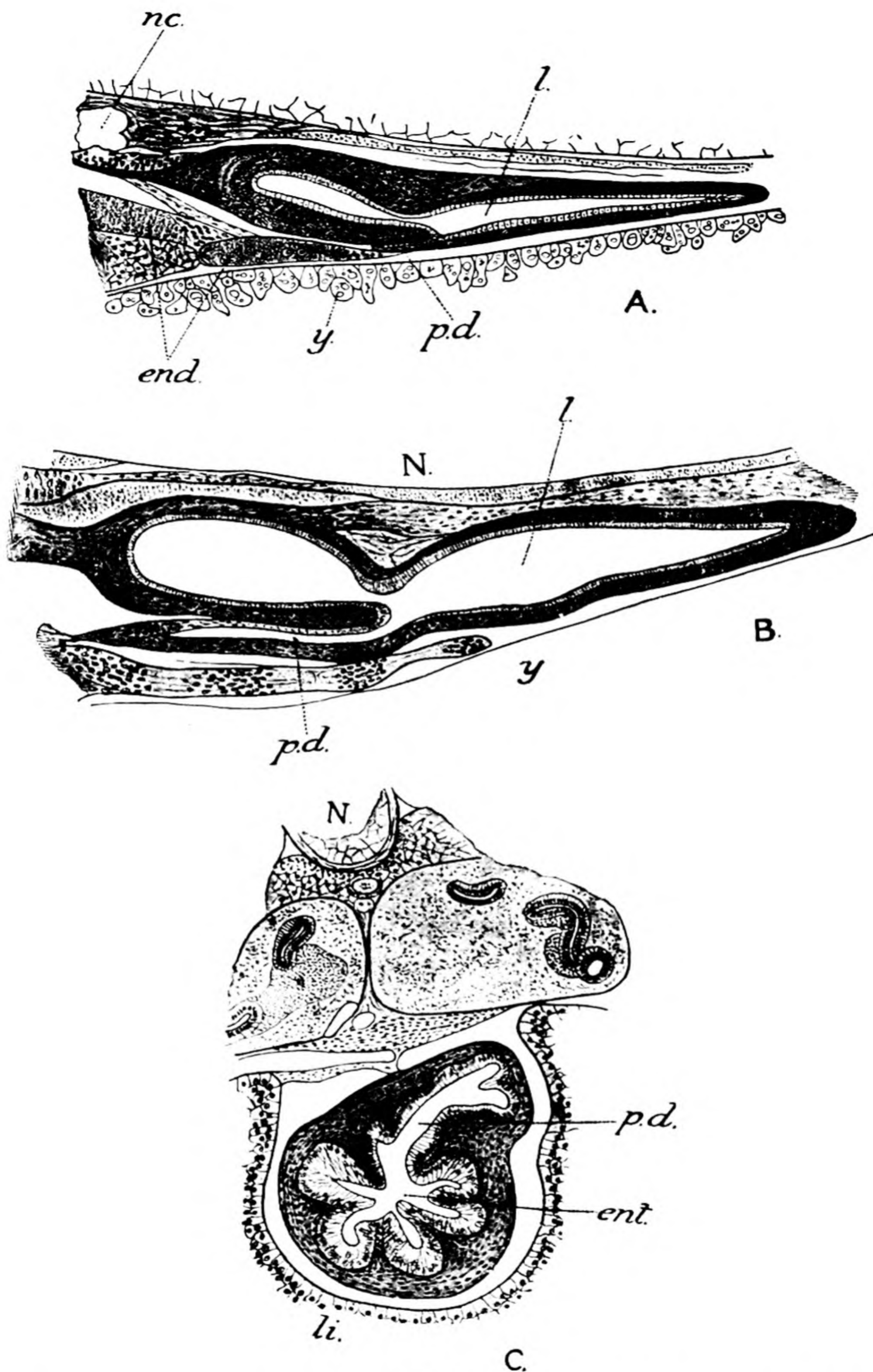
FIG. 589.

Development of the air-bladder of a Teleost. (After Moser, 1904.) A, *Rhodeus*, 5 mm., longitudinal section; B, *Rhodeus*, 6 mm., longitudinal section; C, *Rhodeus*, 7 mm., transverse section, showing small pouch-like outgrowth of pneumatic duct. *end*, Endoderm; *ent*, enteric cavity; *l*, air-bladder; *li*, liver; *N*, notochord; *nc*, pronephric chamber; *p.d*, pneumatic duct; *y*, yolk. (From Kerr, *Embryology*, 1919.)

ductus passes down the mesentery, is short and wide in the lower forms, such as *Amia, Lepidosteus*, and the Chondrostei, but longer and narrower in the Teleostei. In *Lepidosteus* it is provided with a median dorsal muscular vestibule (Wiedersheim, 946). While it usually occurs as an open duct in the lower Teleostei, such as the Clupeiformes, Esociformes, Anguilliformes, and Cypriniformes, the pneumatic duct may become very narrow, reduced to a solid thread, or finally disappear in the more specialised groups. Adult Gasterosteiformes, Mugiliformes, Notacanthiformes, and Acanthopterygii, with few exceptions, have no open duct. The Teleosts were therefore formerly subdivided into the Physostomi with an open duct (J. Müller, 1842) and Physoclisti with a closed bladder (Bonaparte), Figs. 588-9, 593.

FIG. 590.

A, Air-bladder of *Lebiasina limaculata*, opened to show internal cells ; B, stomach of *Ichthyoborus niloticus*, showing entrance of pneumatic duct. *ab*, Anterior division ; *ce*, cellular wall ; *oe*, oesophagus ; *pb*, posterior division ; *pd*, pneumatic duct ; *sp*, pyloric end of stomach ; *st*, stomach. (After Rowntree from Goodrich, *Vert. Craniata*, 1909.)

However, since all these air-bladders develop as diverticula in open communication with the alimentary canal (Rathke, 1827 ; von Baer, 1834), the duct in later stages becoming more or less completely obliterated, and since physoclistous forms occur exceptionally among physostomous groups, and open ducts are retained sometimes in physoclistous groups (Berycidae among the Acanthopterygii), this classification has been abandoned as of little value. As a rule the pneumatic duct opens in the mid-dorsal line in the Actinopterygii ; but in many Teleosts, such as the Salmonidae, Siluridae, Cyprinodontidae, Percopsidae, Galaxiidae, it is somewhat to the right ; while in the Mormyridae, Notopteridae, Gymnotidae, Cyprinidae, Characinidae, it is rather to the left, Fig. 590. Indeed, in *Erythrinus* and Macrodon, belonging to the last family, the

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duct opens well on the left side of the oesophagus (Sagemehl, 378 ; Rowntree, 938).

It is clear that important differences exist between the various kinds of air-bladder found in the Osteichthyes ; but attempts have been made to derive them all from some primitive ancestral form. To Boas we owe the suggestion that an original single dorsal bladder, opening by a median dorsal duct, split into right and left halves, which separated, passed down each side of the gut, and reunited ventrally ; finally opening by a median ventral glottis as in *Polypterus*. There is little, however, to support this view. More plausible is the theory of Sagemehl, according to which, on the contrary, the bladder was originally ventral and bilobed, and shifted round to the right side in the Dipnoi and to the left side in the Actinopterygii. *Erythrinus*, and other fishes in which the duct is on the left, would represent intermediate stages in the shifting of the opening. We shall see that neither of these theories is satisfactory, and that the best solution of this morphological puzzle seems to be afforded by the theory of Spengel (941) based on Goette's original suggestion that the lungs are derived from a posterior pair of branchial pouches. The union of the right and left pouch ventrally would give rise to the condition in *Polypterus* (Dipnoi and Tetrapoda), while their more complete fusion dorsally would yield the single bladder of *Amia* and the other Actinopterygii, Figs. 588, 592.

Concerning the original position of the dorsal opening the evidence of embryology is ambiguous, as the bladder appears to arise sometimes on the right (*Amia*, Piper, 930 ; *Acipenser*, Ballantyne, 886 ; Cyprinoids, Salmonids, Moser, 922), sometimes on the left (Lophobranchs, Weber, '86). These appearances are, however, probably deceptive, and due to differential growth and secondary torsions which are known to occur in the later stages of development. Recently Makuschok has contended, probably rightly, that the dorsal air-bladder always first arises as a diverticulum in the middle line, and that its apparent development on the right side is due to the bending over to the left of the mesentery and gut as it rises off the yolk-sac (919). Of a double origin the embryo shows no distinct trace in Actinopterygians, though Ballantyne has brought forward some evidence of a bifurcation of the rudiment in the embryo. According to her it is the original right lobe which has moved round to a dorsal position, the left disappearing (886).[1] It must

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[1] It has been suggested that the preponderance of the right lobe and reduction of the left is due in large measure to the position of the stomach. Supposed vestiges of the left lobe have been described in *Amia* and *Acipenser* by Ballantyne (886).

be confessed that no convincing intermediate steps between the single dorsal bladder and the paired pouches which are supposed to have given rise to it have yet been discovered (see, however, *Polypterus* below). The problem remains unsolved; nevertheless, Spengel's theory seems to be the most promising.

The blood-supply affords important evidence. It is a remarkable fact that in *Polypterus* and the Dipnoi the blood is supplied to the air-bladder by paired afferent pulmonary arteries coming from the last
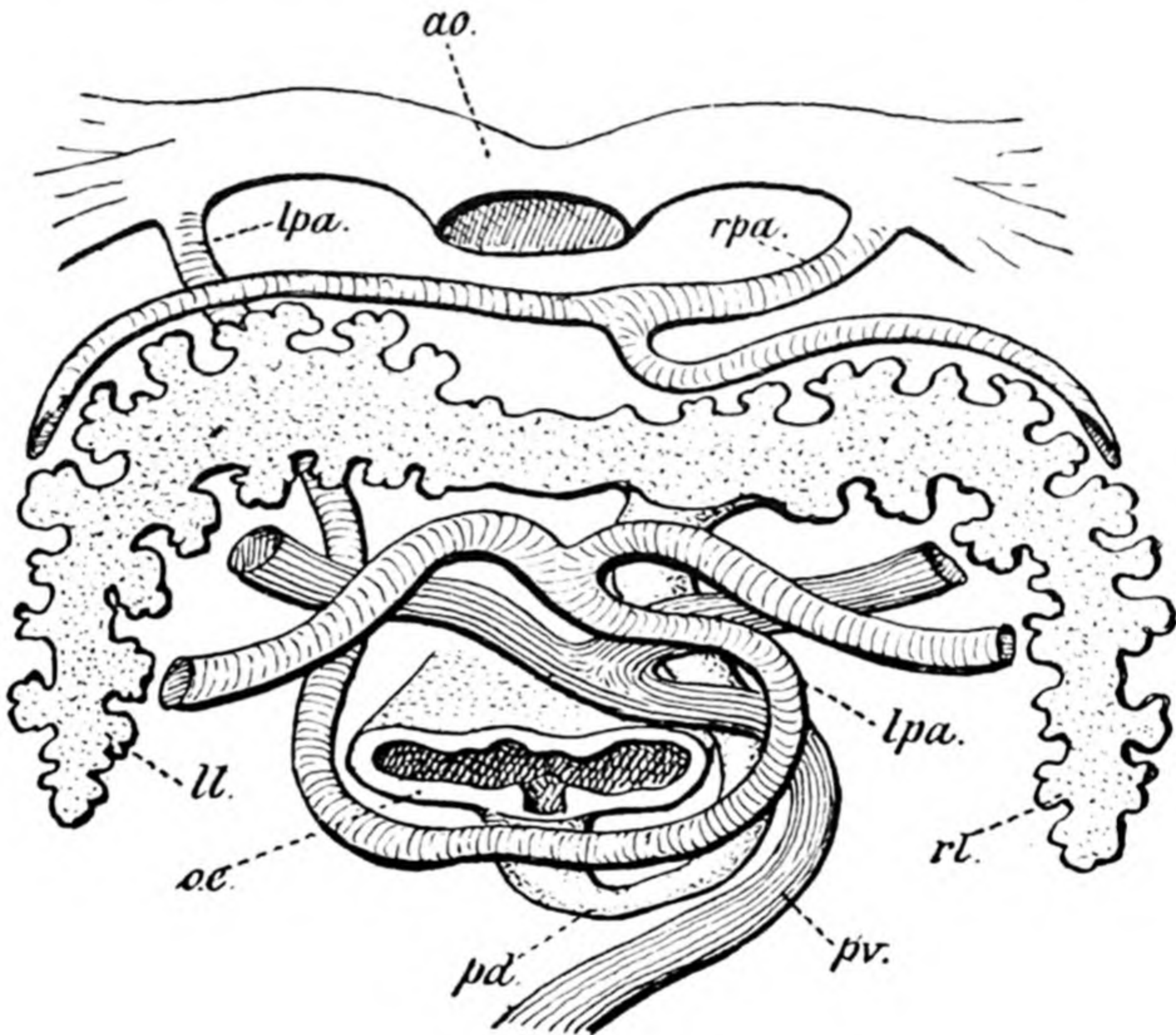
FIG. 591.

Diagram showing the relations of the oesophagus, *oe*, the pneumatic duct, *pd*, the bilobed air-bladder and its blood-supply in *Protopterus*, seen from behind. *ao*, Junction of aortic arches to dorsal aorta; *ll*, left lobe of air-bladder; *lpa*, left pulmonary artery; *pv*, pulmonary vein; *rl*, right lobe of air-bladder; *rpa*, right pulmonary artery. (From Goodrich, *Vert. Craniata*, 1909.)

(fourth) arterial arch, the sixth of the embryonic series. Paired efferent veins return the blood to the hepatic veins near the sinus venosus in *Polypterus*, and directly to the heart in the Dipnoi, where they join to a single pulmonary vein entering on the left side (p. 550). Thus the structure of *Polypterus* is consistent with the theory of Boas, but not with that of Sagemehl. On the other hand, that the bladder of the Dipnoi was originally ventral is proved not only by the course of the left pulmonary vessels, which pass round the oesophagus ventrally together with the duct to reach the now dorsal bladder, but also by the development

of the bladder itself, Figs. 591-2. It arises ventrally and grows round in later stages, so that the original right edge comes to lie on the left (Neumayer, 926; Kerr, 914).[1] The fact that the large right lobe of the air-bladder of *Polypterus* has already come to occupy a dorsal position posteriorly (Kerr, 840) would seem further to support Sagemehl's inter-
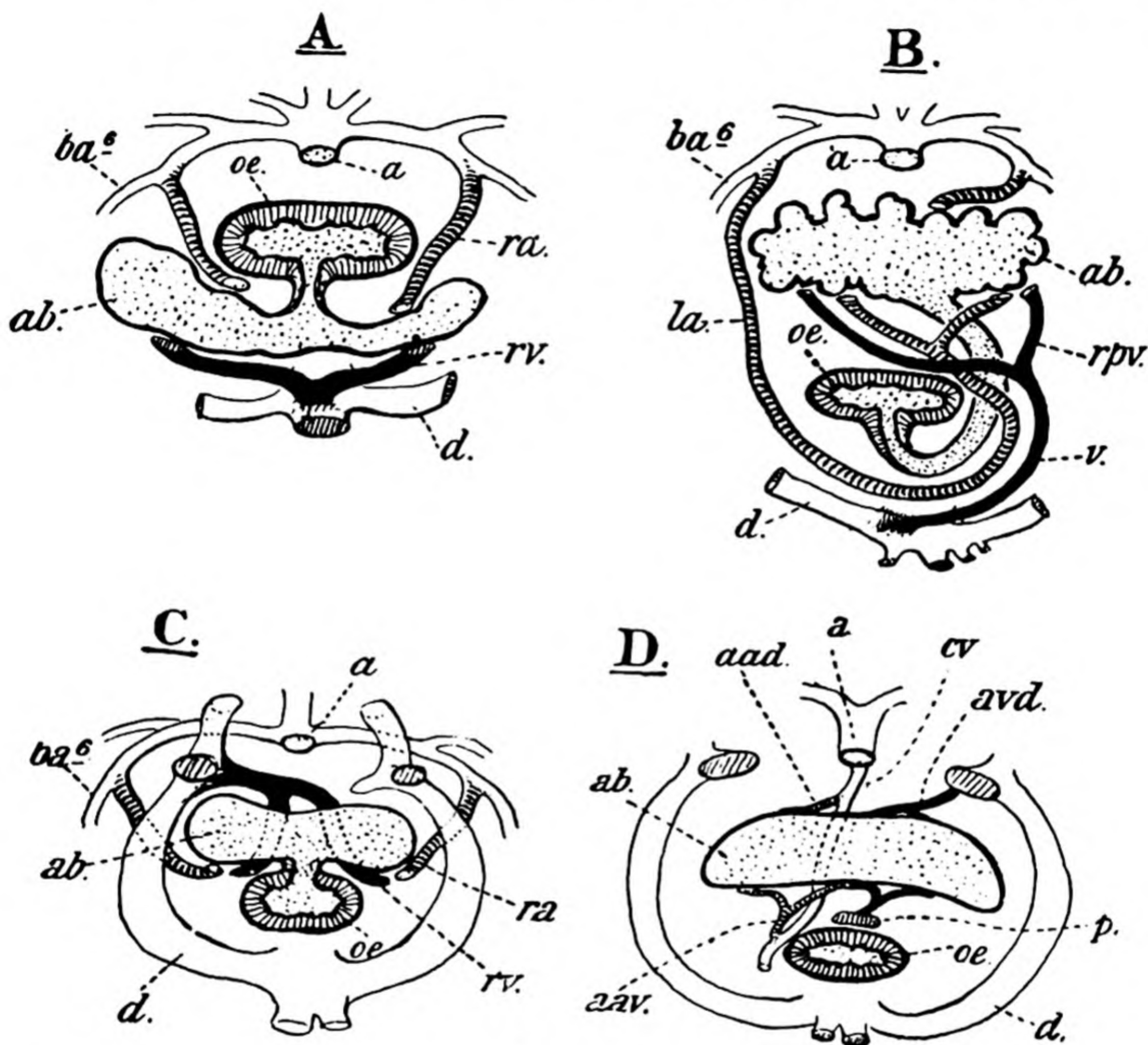
FIG. 592.

Diagrams illustrating the blood-supply of the air-bladder in A, *Polypterus*, B, *Ceratodus*, C, *Amia*, and D, a Teleost. The blood-vessels are seen from behind, and cut short in transverse section. *a*, Dorsal aorta; *aad*, anterior dorsal artery from the coeliac; *aav*, ant. ventral artery; *ab*, air-bladder; *avd*, anterior dorsal vein to the cardinal; *ba⁶*, 4th aortic arch (6th of the series); *cv*, coeliac artery; *d*, ductus Cuvieri; *la*, left pulmonary artery; *oe*, oesophagus; *pr*, portal vein receiving posterior vein from air-bladder; *ra*, right 'pulmonary' artery; *rpv*, right (branch of) 'pulmonary' vein; *rv*, right vein from air-bladder; *v*, left 'pulmonary' vein. (From Goodrich, *Vert. Craniata*, 1909.)

pretation. For it would only be necessary for the left lobe to disappear and for the glottis to shift on to the dorsal side with the shortening duct

[1] The monopneumonous condition of *Ceratodus* is probably due to the suppression of the original left lobe. A small vestige of this lobe has been described in the embryo; it soon merges ventrally with the ductus (Gregg Wilson, 1901; Neumayer, 926; Ballantyne, 886).

But if this vestige has been rightly identified, it is not clear why the left pulmonary artery should pass round to the dorsal lung.

to complete the Actinopterygian structure ; the shifting would be to the right, however, instead of the left side. But we now meet with a serious and perhaps fatal difficulty in *Amia*. For here, while the bladder and opening of the duct are median and dorsal, the blood-supply is essentially bilaterally symmetrical. It is true that the efferent veins join and enter the left ductus Cuvieri ; but *Amia* alone among the Actinopterygii has its bladder supplied by a right and left pulmonary artery from the last pair of arterial arches. There can, therefore, apparently have been no shifting of the bladder either to the right or the left, Fig. 592 c.

In all other Actinopterygii the air-bladder receives its blood from the dorsal aorta or its branches. Concerning the possibility of a change of arterial supply from branchial aortic arch to dorsal aorta or coeliac artery, interesting evidence may be derived from the development of *Gymnarchus*. Whereas in early stages the air-bladder receives blood from the posterior aortic arches on the left and the combined arches and coeliac on the right side, in later stages the coeliac and pulmonary arise from the aorta (Assheton, 885 ; Ballantyne, 886).

Important also is the nerve-supply, first studied by Czermack, 1850. The dorsal bladder of Actinopterygians appears to be always innervated from both the right and left vagus. Must it not, therefore, have preserved its original position ? Kerr has shown that in Dipnoi, where the left vagus does not pass round ventrally (like the pulmonary artery) but dorsally to the oesophagus, and crossing over the right vagus passes to the right side of the bladder, this strange condition must be due to secondary anastomosis. For in *Polypterus* also the branch of the left vagus crosses over the oesophagus to the large right lobe of the air-bladder ; although, of course, in this fish there has certainly been no shifting of the bladder from one side to the other. It follows that nerve-supply is no certain guide to the phylogenetic history of the air-bladder, but may be re-adjusted to suit varying adaptations (Kerr, 914).

About the functions of the Actinopterygian air-bladder there has been much controversy ever since Rondelet, in 1554, maintained that it helps the fish to swim. More than a century later Needham (1667) discussed the possibility of its serving as a float, a respiratory reservoir of air, or an organ secreting gas to help in digestion. Boyle, Mayow, Ray, Borelli, and many others in the seventeenth century studied the question experimentally, and the discussion was carried on with much zeal throughout the eighteenth and nineteenth centuries. Perrault (1680) and Monro (1785) showed that gas is secreted by the red gland in closed bladders ; and a few years later Priestley, Fourclay, Brodbelt, Lacépède, and Biot analysed the gas and found that the proportion of oxygen varies greatly,

and is often greater than in air. Biot found that almost pure oxygen fills the bladder of deep-sea fish. Hitherto the bladder had been generally held to act as a hydrostatic organ enabling the fish to rise and sink ; but in 1809 Provencal and Humboldt pointed out that a fish can swim well after its bladder has been punctured or even removed. Delaroche (1809), and
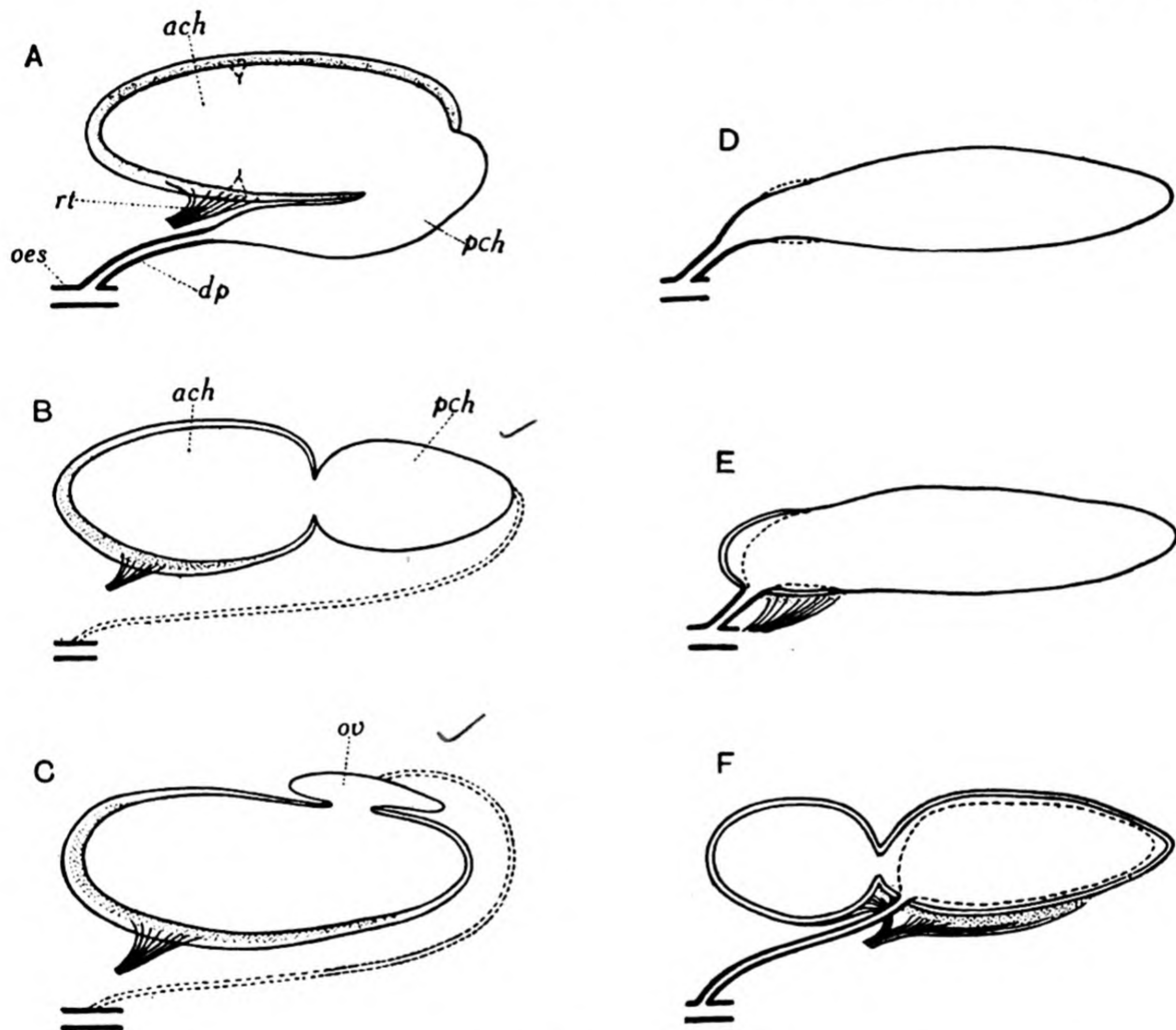
FIG. 593.

Diagram of various types of *air-bladder* found in *Teleostei* (from M. Rauther, 1923). A, Hypothetical ; B, physoclistous with posterior chamber, and C, with oval ; D, Salmonid ; E, Esocid ; F, Cyprinoid. *ach*, Anterior gas-secreting chamber ; *dp*, ductus pneumaticus ; *oes*, oesophagus ; *ov*, gas-absorbing oval ; *pch*, posterior chamber ; *rt*, rete mirabile related to gas-gland.

later Moreau (1876), did much to establish the modern view, according to which the air-bladder in the Teleostei does not actively cause the fish to rise and sink, this rapid vertical motion being brought about by means of the fins, but enables it so to alter its specific gravity as to keep it approximately equal to that of the water at any desired level. By varying the amount of gas inside the bladder and adjusting it to the pressure from outside, the fish is kept in a state of equilibrium in which it can maintain

itself with minimum exertion in a plane of least effort (Hall, 907 ; Tower, 1902 ; Baglioni, 1908 ; Popta, 1910–12 ; Guyénot, 1909–12).

Further evidence that the bladder acts thus as an adjustable float is afforded by the fact that most of the Teleosts which have lost it are bottom-living forms, as for instance the Pleuronectidae. Cunningham has made the interesting observation that in *Rhombus* the bladder is present in the free-swimming larva, and it has since been found to occur in the young of other Pleuronectids and of *Uranoscopus* (Ehrenbaum, 1896 ; Thilo, 1899–1914).

Some fish with an open pneumatic duct can fill the bladder by swallowing air from the surface; but as a rule the gas is secreted from the blood, and the duct serves rather as a safety valve to let
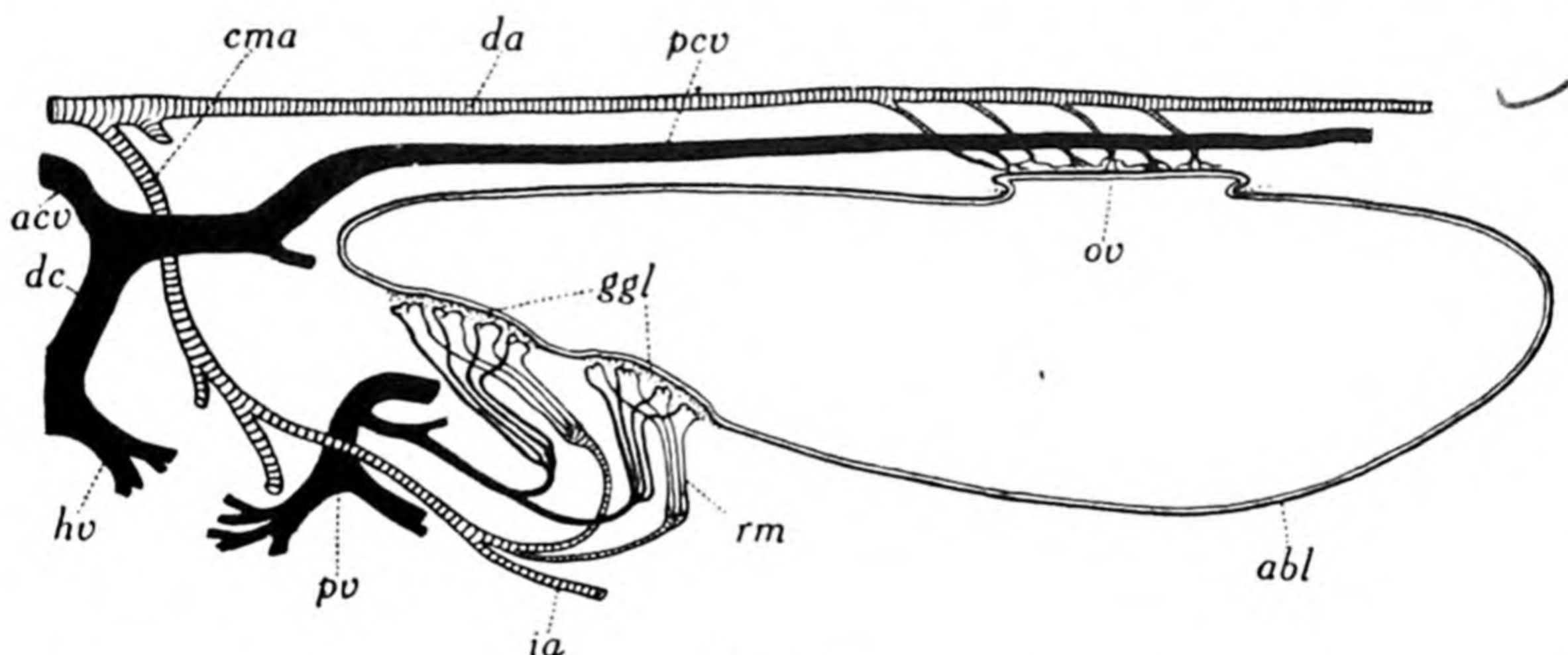
Fig. 594.

Diagram of blood-supply to physoclistous *Teleostean air-bladder* ; left-side view. Veins black, arteries cross-lined. *abl*, Air bladder ; *acv*, anterior cardinal ; *cma*, coeliaco-mesenteric ; *da*, dorsal aorta ; *dc*, ductus Cuvieri ; *ggl*, gas-gland ; *hv*, hepatic ; *ia*, intestinal ; *ov*, oval ; *pcv*, posterior cardinal ; *pv*, portal ; *rm*, rete mirabile.

out excess. The fact that oxygen can be much more easily secreted and absorbed than nitrogen accounts for the presence of oxygen in large and very variable proportion. The secretion of gas may take place in less specialised forms from the general inner surface of the bladder (ventral surface in Cypriniformes, anterior surface in most Clupeiformes), or from a special area of the wall (de Beaufort, 887 ; Rauther, 932). There is a tendency for the bladder to become differentiated into an anterior oxygen-producing and a posterior oxygen-absorbing region. Further, a special area in the former becomes differentiated for secreting gas and is known as the red body (Monro, 1785). This consists of the internal oxygen-secreting epithelium and a capillary network on the wall of the bladder together forming the gas gland proper, in more or less close connexion with a rete mirabile, a wonderfully complex structure of venous and arterial capillaries which do not communicate until they reach

the gland (J. Müller, 1840–42 ; Quekett, 1842–4 ; Corning, 896 ; Woodland, 949-50). The more primitive structure, found in physostomous fishes, in which the gland is covered with simple flat epithelium, has been named (together with its rete mirabile) the red body, while the higher type found in physoclistous fishes, in which the gland is covered with thick glandular
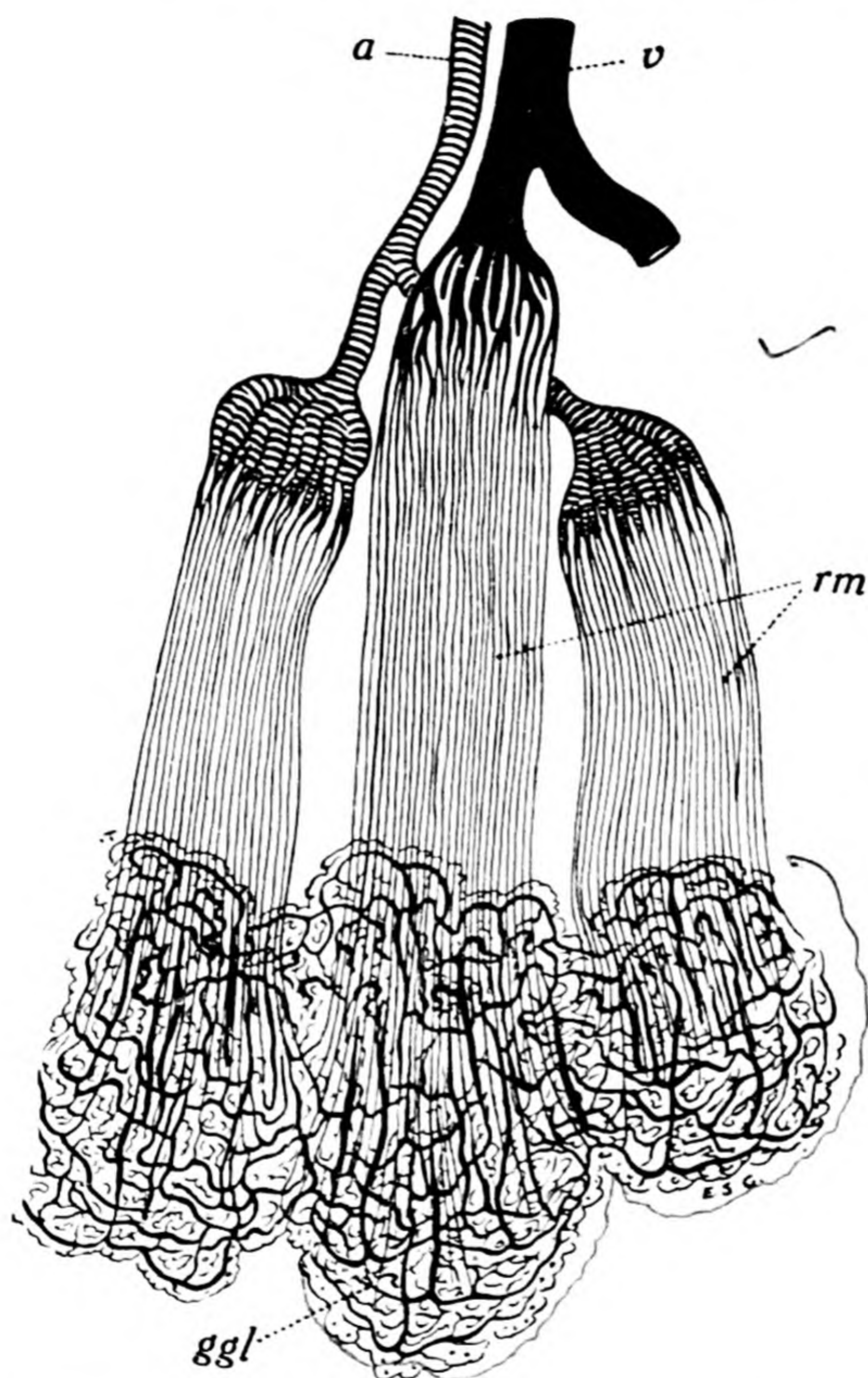
FIG. 595.

Labrus bergylta, portion of gas-gland, *ggl*, with vascular supply. *a*, Artery ; *rm*, rete mirabile ; *v*, vein.

epithelium thrown into folds or sunk in crypts, is named red gland (Coggi, 895 ; Vincent and Barnes, 844 ; Nusbaum, 928 ; Reis and Nusbaum, 933 ; Haldane, 906 ; Woodland, 849). The remainder of the anterior chamber is lined with thick impermeable tissue, covered internally with simple epithelium, Figs. 593-7.

The posterior oxygen-absorbing region, derived apparently from the embryonic pneumatic duct itself, in physoclistous fishes is lined by a thin epithelium through which oxygen can easily pass to the rich network of vessels overlying it (Tracy, 942).

In still more specialised forms, such as *Mugil*, *Balistes*, and the Gadidae, this posterior region becomes converted into a flattened 'oval' which can be closed off by a circular fold provided with sphincter and dilator muscles (Tracy, Woodland, Reis and Nusbaum).

While the red glands are supplied from the coeliac artery and return their venous blood to the portal vein, the absorptive region and 'oval'

FIG. 596.

Inner view of anterior end of air-bladder of *Labrus bergylta*, seen from behind. *ab*, Cut wall; *blv*, blood-vessel; *ggl*, gas-gland.

receive branches from the dorsal aorta and return their venous blood to the posterior cardinals (Corning, 896). Moreover, secretion of oxygen would seem to be controlled by the vagus and absorption by the sympathetic (Bohr, 889). Thus can the pressure of oxygen inside even the closed air-bladder be delicately regulated, and if necessary be made vastly superior to its pressure outside or in the blood by the active participation of the glandular cells.

The air-bladder undergoes many strange modifications in the Teleostei. It acquires a second opening to the exterior near the anus in many Clupeids such as the herring, *Clupea harengus*, *Pellona*, *Sardinella* (de Beaufort, 887), and in the horse-mackerel, *Caranx trachurus*,

FIG. 597.

Inner view of roof of air-bladder of *Mugil chelo*, showing oval. *cm*, Circular closing muscles; *fe*, folded epithelium of oxygen-absorbing area; *m*, rim of oval pocket; *rm*, radiating opening muscles.

a small opening into the right branchial cavity. Often the bladder is provided with lobes and branches, sometimes of great complexity and of doubtful function (Gunther, 1880). They sometimes actually push

their way into the perilymph cavity of the auditory capsule, Fig. 598 (Weber, 1820; Parker, 929; Ridewood, 934; de Beaufort, 887; Tracy, 943). In *Megalops* these diverticula are lodged in bony bullae of the pro-otic, in *Notopterus* they are separated from the perilymph by membrane alone, while in Hyodon they plunge into the perilymph itself. The diverticula in Clupeidae may pass ventrally beyond the labyrinth, and in Mormyridae may be applied to the wall
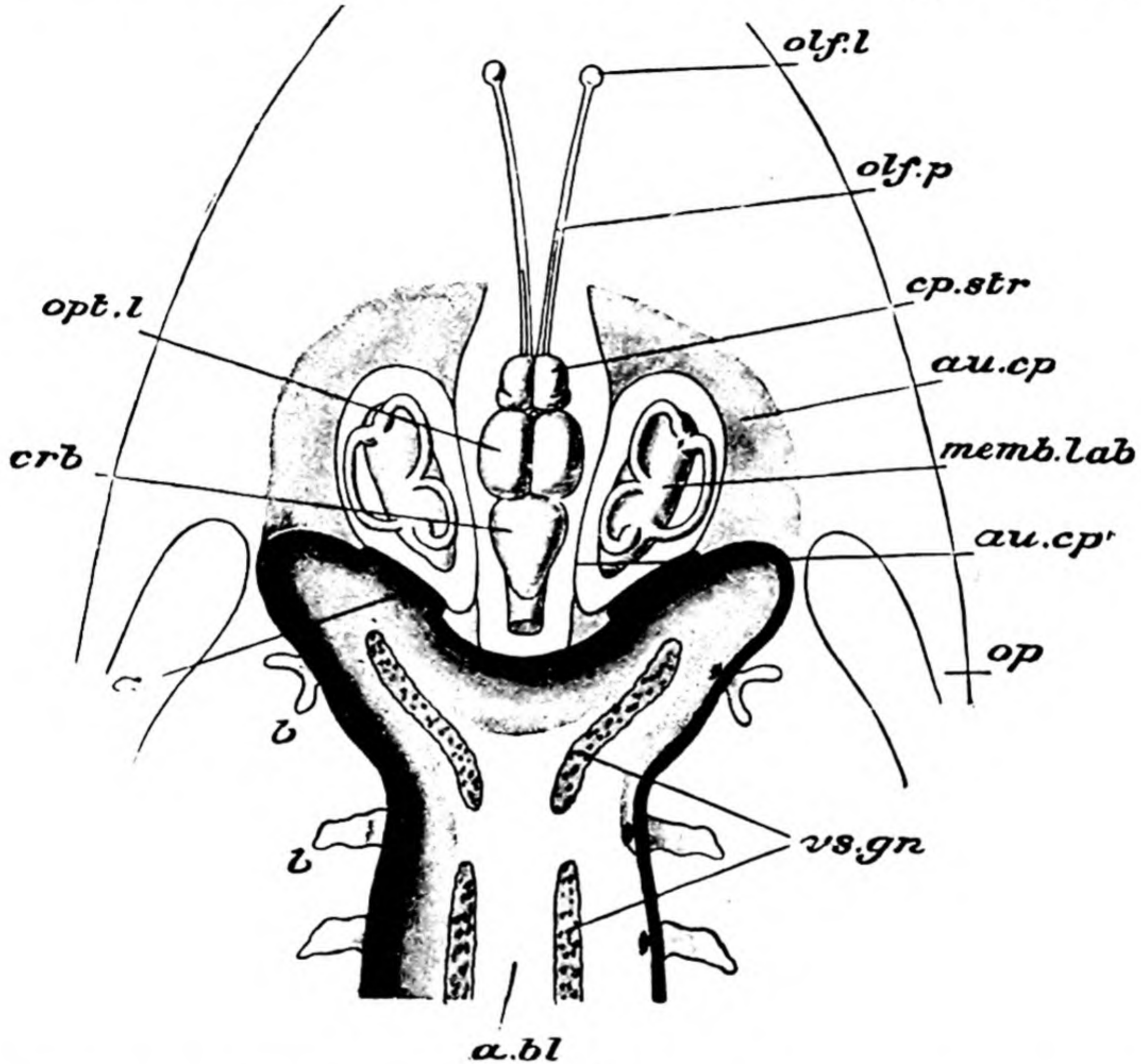
FIG. 598.

Horizontal section of posterior portion of head and anterior end of air-bladder in *Pseudophycis bachus*, one of the Gadidae or Cods (semi-diagrammatic). *a*, Thickened portion of air-bladder fitting into fenestra in posterior wall of auditory capsule; *a.bl*, air-bladder; *au.cp*, outer wall of auditory capsule; *au.cp'*, inner (membranous) wall; *b*, hollow offshoots of air-bladder; *cp.str*, corpora striata; *crb*, cerebellum; *memb.lab*, membranous labyrinth; *olf.l*, olfactory bulbs; *olf.p*, olfactory peduncles (olfactory tracts); *op*, operculum; *opt.l*, optic lobes; *vs.gn*, vaso-ganglia. (From Parker and Haswell, *Zoology*.)

of the sacculus. (But by far the most interesting form of connexion between the bladder and the ear is that described by Weber in 1820, and which occurs in all the Cypriniformes (Ostariophysi), Figs. 599, 600. Here the bladder is enabled to communicate pressure to the perilymph by means of a series of ossicles compared by Weber to the ear ossicles of the mammal, but now known to be of quite different origin and to be formed by the specialisation of portions of the anterior vertebral segments,

as first suggested by Geoffroy Saint-Hilaire, 1824. Accompanying the chain of ossicles is a singular modification of the ear itself. The right and
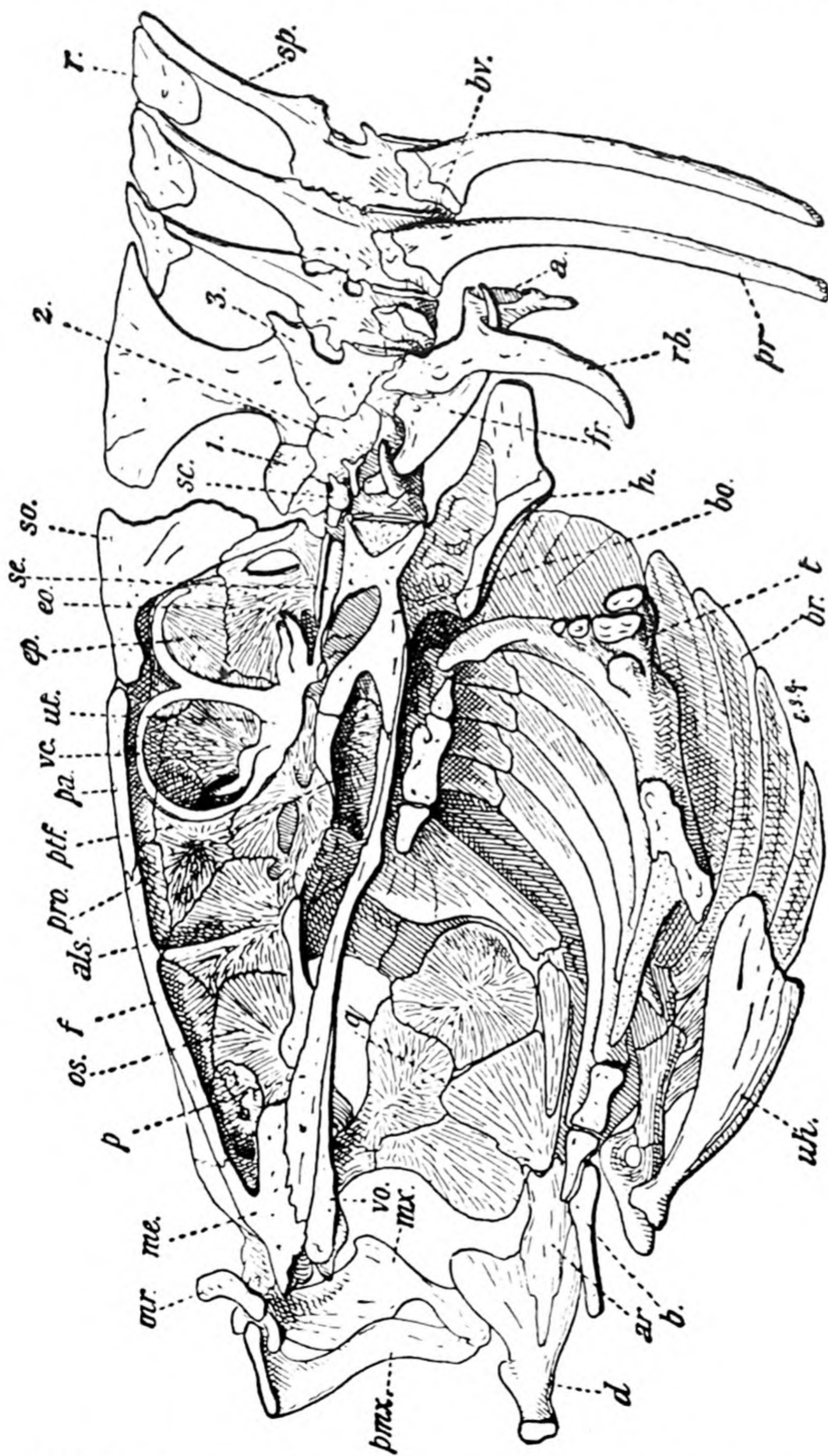
FIG. 599.

Cyprinus carpio, L. Skull and visceral arches cut in half, and first few vertebrae. Weberian ossicles are shown; the rib of the fourth vertebra has been removed. *a*, Surface of modified third rib, which presses on air-bladder; *als*, pterosphenoid; *ar*, articular; *b*, basihyal; *bo*, basioccipital; *br*, branchiostegal ray; *bv*, basiventral (parapophysis); *d*, dentary; *eo*, exoccipital, below it roofs over the sinus; *ep*, epiotic; *f*, frontal; *fr*, tripus; *h*, horny pad on masticating process of basioccipital; *me*, mesethmoid; *mr*, median rostral; *mx*, maxilla; *os*, orbitosphenoid; *p*, parasphenoid; *pa*, parietal; *pmx*, premaxilla; *pr*, pleural rib; *pro*, eye-muscle canal partly roofed over by pro-otic; *ptf*, postfrontal; *q*, quadrate; *r*, radial; *rb*, modified rib; *sc*, scaphium, with intercalarium below it; *se*, median sinus endolymphaticus; *so*, supraoccipital; *sp*, neural spine; *t*, teeth on fifth branchial arch; *uh*, urohyal; *ut*, utriculus; *vc*, vertical semicircular canal; *vo*, voner; 1, 2, 3, elements of first three vertebrae, 1 and 3 probably neural arches, 2 possibly basiventral. (From Goodrich, *Vert. Craniata*, 1909.)

left perilymph cavities become continuous below the brain, and the two membranous labyrinths join to a median canal from which arise and pass

backwards two sacculi and a median sinus endolymphaticus. The latter is lodged in an extension of the perilymph cavity excavated in the basioccipital. (The structure of Weber's apparatus is fairly constant throughout the Cypriniformes and consists usually of a large malleus connected with the front wall of the bladder, joined by a small incus to a stapes fitting into the atrial fenestra, and a claustrum lying on the membranous wall of the atrium) for these misleading names Bridge and Haddon have proposed the terms: tripus (malleus), intercalarium (incus), scaphium (stapes), which we shall adopt.

Various attempts have been made to trace out the exact homology of the ossicles. A. Müller (1853) first derived the scaphium from neural arch 1, the intercalarium from neural arch 2, and the tripus from the rib of the third vertebra; and his conclusions have been in the main confirmed by subsequent observers (Nusbaum, 927; R. Wright, 951; Bridge and Haddon, 891; Bloch, 888). But the question is complicated by the assimilation of vertebrae to the occipital region of the skull (Sagemehl, 378), and by the formation of rigid compound vertebrae behind the skull by the fusion of centra. Thus three vertebrae may fuse in Cyprinids, and as many as five in Siluroids
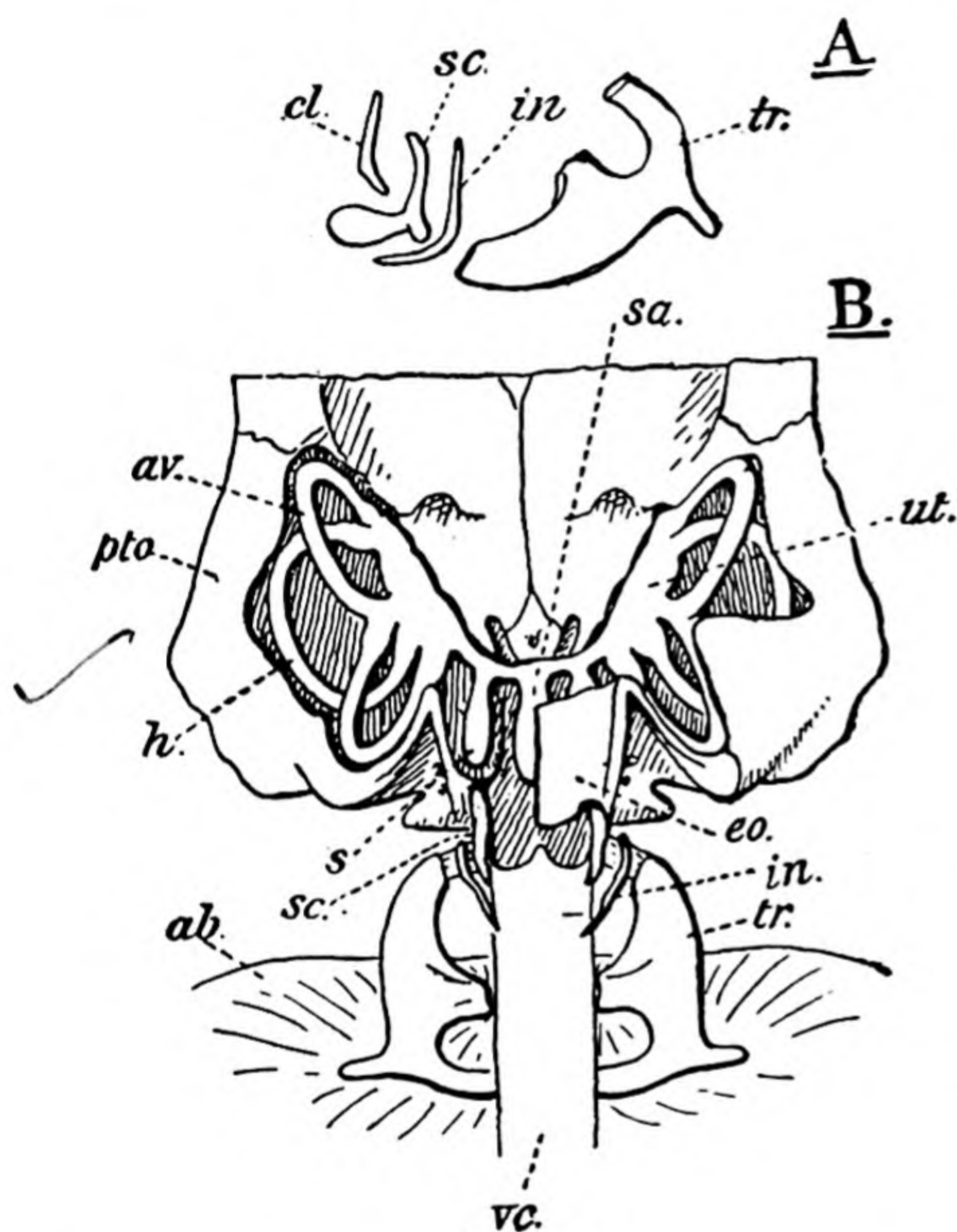
FIG. 600.

Macrones nemurus. A, The Weberian ossicles; B, portion of the skull, the labyrinth, and Weberian apparatus diagrammatically represented from above (from the figures of Bridge and Haddon). *ab,* Air-bladder; *av,* anterior vertical canal of the ear; *cl,* claustrum; *eo,* exoccipital; *h,* horizontal canal; *in,* intercalarium; *pto,* pterotic; *s,* sacculus; *sc,* scaphium; *tr,* tripus; *ut,* utriculus; *vc,* vertebral column. (From Goodrich, *Vert. Craniata,* 1909.)

(Wright, 951). According to Nusbaum's recent account in *Cyprinus* three vertebral segments combine with the skull behind the vagus foramen to form the basioccipital region, and the haemal arches of the second and third fuse to form the large ventral masticatory process enclosing the aorta, while their neural spines contribute to the supraoccipital. The neural arch of the third of these segments forms the scaphium, that of the first post-occipital segment the intercalarium, and the haemal arch

(probably including the rib) the tripus. The claustrum, when present, would be derived from the intercalary of that segment (Wright, 951). The Cypriniformes, especially the Siluroids, often have a highly modified air-bladder, reduced in size, and sometimes partially enclosed in bony expansions of the vertebrae or ossified (see Bridge and Haddon, 891 ; Sörensen, 939 ; Bloch, 888). In many Cyprinidae, Characinidae, and Siluridae the bladder has paired extensions passing outwards to below the skin, forming a sort of tympanum behind the pectoral girdle.

Sörensen supports Weber's original suggestion that the apparatus serves to intensify sound vibrations and carry them to the ear, while also holding that it assists in the production of sounds by the fish. Hasse (909), on the other hand, considers that it acquaints the fish with the state of tension of the air in its bladder at various depths. When the air-bladder expands the stapes or scaphium is pushed in ; when it contracts the scaphium is drawn out. Although it cannot yet be held that the function of Weber's apparatus has been thoroughly determined, yet it seems highly probable that, as Sagemehl (378) suggested, it transmits changes of pressure to the perilymph, and sets up reflex actions which allow gas to escape by the duct or be secreted into the bladder (Evans, 897 ; Evans and Damant, 898 ; Guyénot, 905).

It may further be noticed that the wall of the air-bladder is generally provided with a layer of smooth splanchnic muscle fibres, and in addition with extrinsic striated muscles supplied by anterior spinal nerves. These muscles seem to have little to do with the altering of the capacity of the bladder for hydrostatic purposes, but are specially developed in those fishes which emit sounds, such as *Zeus, Dactylopterus, Trigla* (Delaroche, 1809). An elaborate sound-producing organ known as the elastic spring apparatus is developed from the modified transverse processes of the fourth vertebra in connexion with the bladder in certain Siluroids (*Auchenipterus, Doras*, etc.; see Sörensen, 939 ; Bridge and Haddon, 891).

Summary.—We may conclude, then, that the functions of the air-bladder in fishes are many and various, but that it acts chiefly as an adjustable float to enable the fish to swim at any level with the least effort. But even among the Teleosts it sometimes acts also as a reserve of oxygen to be drawn upon in case of special need (Jacobs, 1898; Moreau, 1876–7). On the whole, it seems probable that the original function of the bladder was respiratory. A cellular lung-like bladder occurs in *Amia, Lepidosteus,* and less developed in certain Teleosts, such as *Megalops, Chirocentrus, Gymnarchus, Arapaima,* and Cyprinoids, Fig. 590 (Wiedersheim, 310a; de Beaufort, 887). Hyrtl (1856) showed that the bladder acts as a lung in *Gymnarchus,* and Jobert (1878) did
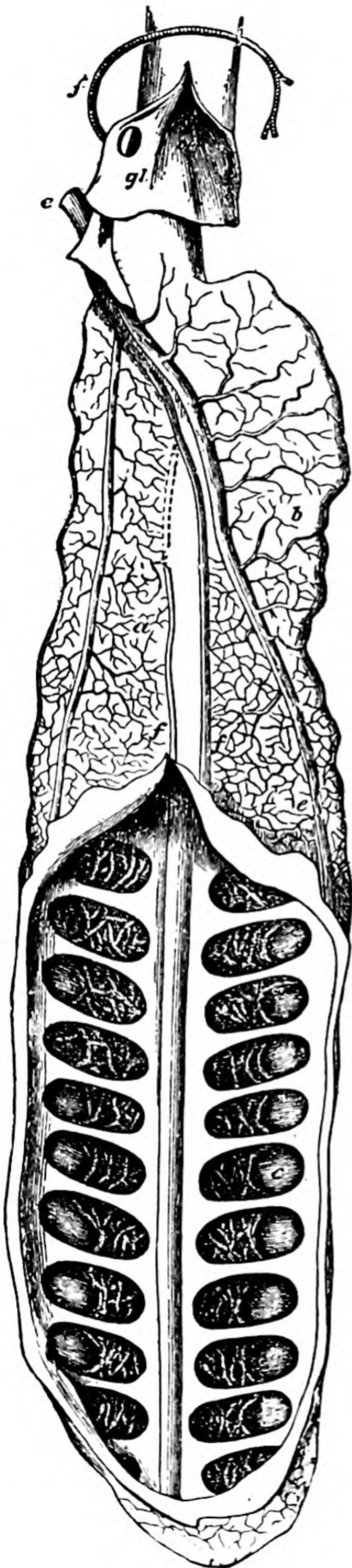
Air-bladder of *Ceratodus Forsteri*, Kr. Opened at its hinder end to show its cellular structure. *a*, Right, and *b*, left side of bladder; *c*, cellular pouch; *e*, pulmonary vein; *f*, pulmonary artery; *gl*, glottis exposed by opening the oesophagus, *oe*. (After Günther.)

the same for *Erythrinus*; nevertheless, it is possible that the lung-like function and structure has been reacquired in these Teleosts as a special adaptation for living in foul water. Such an explanation, however, does not appear to apply to the more primitive fish, like *Polypterus*, *Amia*, and *Lepidosteus*, where the respiratory function seems to be primary (Mark, 1890; Budgett, 776; Potter, 931). That the bladder of the Dipnoi resembles a lung both in structure and in function has long been known, Fig. 601, and in *Protopterus* the air-cells are more elaborately developed than in many Amphibia (Parker, 929; Spencer, 940).

As for the origin of the air-bladder, we may conclude that it was probably derived from a posterior pair of gill-pouches, although it must be confessed that so far no definite embryological evidence of this has been found. This theory alone accounts for the blood-supply from the arterial arch in Dipnoi, *Polypterus*, and *Amia*, and overcomes the difficulty of explaining the initial stages in phylogeny. Presumably when, in the Actinopterygii, either one or both of the pouches became dorsal and converted into a float into which gas was secreted, the arterial blood-supply was drawn more directly from the aorta. Moreover, the theory of Spengel, already referred to (941), is supported by the latest views on the first origin of lungs.

THE LUNGS OF TETRAPODA

That the lungs of the land vertebrates were originally derived from gill-pouches was suggested many years ago by Goette (1875), who showed that in *Pelobates* they arise from paired rudiments. Nevertheless, it has generally been held that the lungs of the Tetrapods develop as a median ventral diverticulum from which grow out a right and left lobe, and this is still stated to be the case in man and in the pig (Flint, 900). Recently, however, much evidence has been brought forward to prove that in all

Tetrapods the earliest trace of the lungs is in the form of paired pouches of the endoderm close behind the last-formed gill-slits, Fig. 604. Weber and Buvignier (945), Greil (903), and Makuschok (918-19) have shown that in Urodela and Anura there is developed behind the vestigial sixth pair of gill-pouches yet another pair of outgrowths, which soon join a median ventral depression, developed immediately in front, either at the same time or very soon after, and representing the rudiment of the larynx and trachea, Figs. 602-3. The tracheo-laryngeal groove, carrying the lungs with it, closes off from behind forwards, leaving the open glottis in front. This mode of development has now been followed not only in Amphibia, but also in Reptilia (Hochstetter, 1906), in Aves (Katschenko, 788 ; Rösler, 937 ; Locy and Larsell, 916), and in Mammalia (Fol ; Weber and Buvignier, 945). Nevertheless, some differences of opinion still persist as to the homology of the lungs. Greil con-

Fig. 602.

Diagram illustrating modification of gill-pouches in phylogeny of *Amphibia* (from M. Makuschok, *Anat. Anz.*, 1914). 1-6, Gill-pouches and slits ; *Ls*, lungs = 7th pair of pouches.

siders that the rudiments are not truly comparable to gill-pouches, being according to him more ventral and sometimes appearing before the last pair ; while Weber and Buvignier believe that they represent rather a reappearance of ancestral pouches than a persistent seventh pair. But although the sixth pair may be delayed in development in Amphibia, there can be little doubt that Makuschok is right in insisting that the lung rudiments are true gill-pouches. Just as in the case of the air-bladder, no other view harmonises so well with the fact that the afferent pulmonary vessel comes from the ventral aorta by way of the sixth embryonic aortic

arch, or gets over so easily the difficulty of explaining the initial stages in phylogeny. For it is easy to imagine that an endodermal gill-pouch might, like the vestigial and evanescent sixth pair, fail to fuse with the ectoderm and remain as blind sacs in which air could be lodged. Real
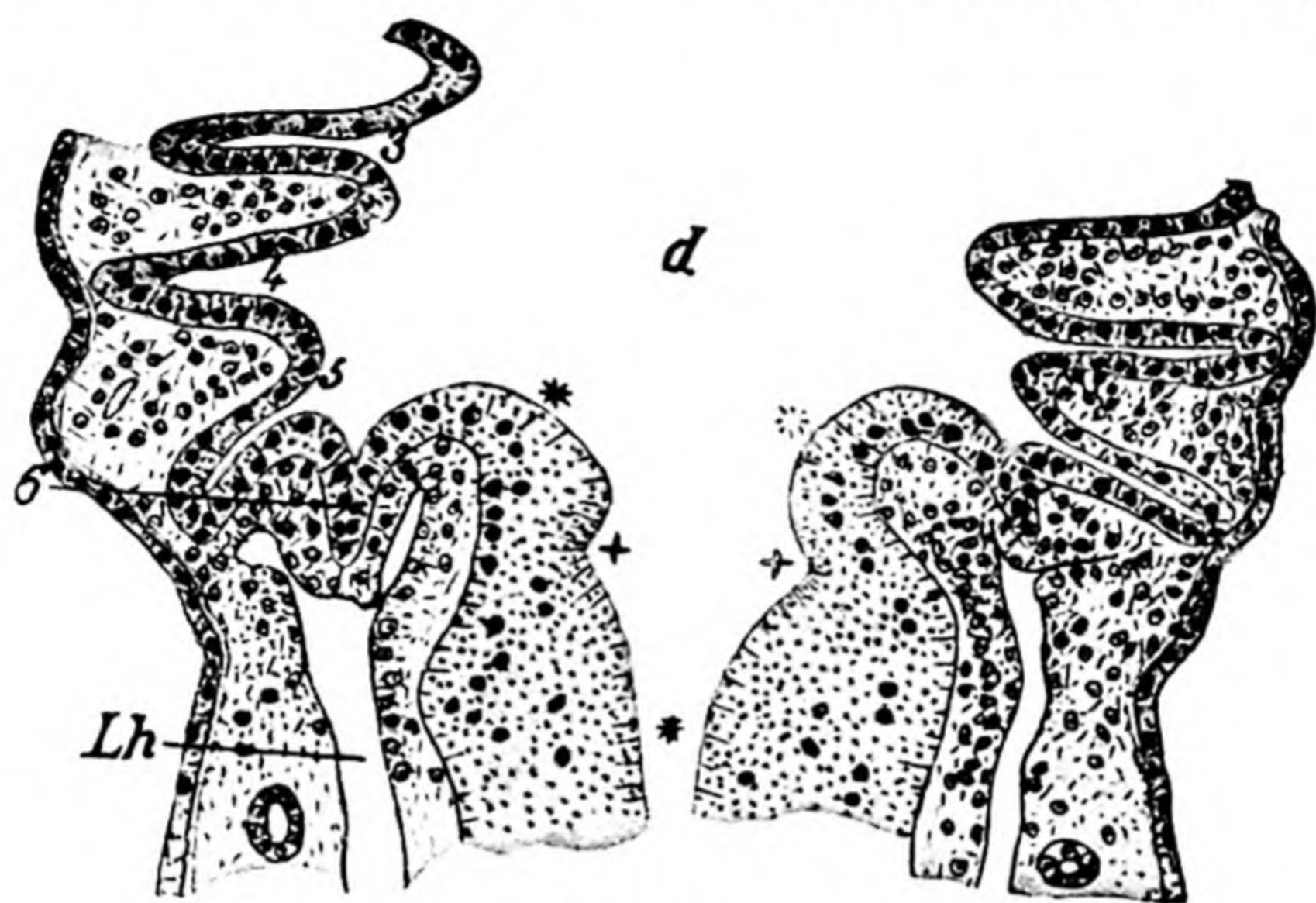
FIG. 603.

Horizontal section through posterior region of pharynx of embryo *Triton* (from M. Makuschok, *Anat. Anz.*, 1911). *d*, Cavity of pharynx; *Lh*, splanchnocoele; 3, 4, 5, developing gill-slits; 6, vestigial sixth slit; +, rudiment of lung diverticula.

intermediate stages we could only expect to find in the long extinct ancestors of the Amphibia.

The organs of respiration undergo most interesting changes in the different classes of the Tetrapoda, and we may now briefly consider

FIG. 604.

Transverse section of embryo *Gallus domesticus*, 24 somite stage (from Rösler, 1911), showing earliest paired rudiments of lungs, *l*. *c*, Splanchnic coelom; *ph*, pharynx.

their structure (Oppel, **795**). We believe the lung of terrestrial Vertebrates to have started from a simple bilobed sac, not unlike that of *Polypterus*, with a vestibule in front opening by the glottis on the floor of the pharynx; the wall was thin, highly vascular, and covered outside by coelomic epithelium, contained smooth muscle fibres supplied by twigs of the vagus; the lining epithelium was ciliated, except in special regions where it was thin and flattened over the capillaries to allow easier respiratory exchange.

Amphibia.—The lungs of the Amphibia have departed but little from this condition; but the vestibule becomes differentiated into a larynx (Göppert, **687, 902**; Wilder, **947**), and a stiff trachea becomes more or less distinctly marked off from the thin-walled distensible lung, the inner wall of which may be thrown into folds. In some Urodeles, such as *Necturus*,

Proteus, and *Triton*, where the lung is rather hydrostatic than respiratory in function (Camerano, 893), the inner surface is smooth. This may, however, be due to secondary simplification. But in others, and especially the Anura, the folds may be increased in depth, and the cavity of the lung be subdivided peripherally by primary and secondary trabeculae into large chambers and smaller irregular air-cells amply supplied with capillaries and affording a large respiratory surface. As a rule the trachea is little differentiated; but in the Gymnophiona and some Urodela (*Siren, Amphiuma*) it is definitely formed, and its wall strengthened by a series of paired cartilages, amounting to semi-rings in the former group.

Between the Amniota and the Amphibia there is an important divergence in the mechanism of respiration; for while in the former the lungs are filled according to the principle of a suction pump, in the latter the action is like that of a force pump. Townson (1794–5) was the first to study the mechanism in the Amphibia, which has since been worked out in detail by various authors (Cuvier, 1835; Haro, 1842; Panizza, 1845; Milne-Edwards, 1857; P. Bert, 1869; Gaupp, 821). But oxygenation of the blood takes place in the Amphibia not only in the lungs, but also in the buccal cavity, the lining of which is usually very vascular, and to an even greater extent in the skin, likewise well supplied with blood-vessels (Williams, 1859). For buccal respiration the glottis is closed, and water or air passed in and out of the buccal cavity through the nostrils by depressing and raising the floor of the buccal cavity.

The process of pulmonary respiration in the frog is as follows (Dakin, 1927). The mouth is kept shut, and at intervals the nostrils are closed and the buccal cavity enlarged by the action of muscles which depress the hyoid plate in its floor. Air is thus drawn out of the lungs and mixed with fresh air present in the buccal cavity. The elevation of the plate and floor of the buccal cavity now forces mixed air into the lungs through the open glottis. The nostrils are closed by pressure of the lower jaw in the Anura or by special valves in the Urodela (Wilder, 947; Anton, 884; Bruner, 892). The lungs behave as passive distensible sacs, though the contractility of their walls may help in expiration. Accompanying this peculiar mode of respiration in which the ribs take no part is their great reduction; in no living Amphibia do they meet the sternum (p. 78).

Before leaving the subject of the lungs in Amphibia, something must be said about the remarkable lungless Urodelous Amphibians recently described by Wilder (948) and Camerano (893). In various species and genera of the family Salamandridae (*Salamandrina, Plethodon, Spelerpes, Batrachoseps, Manculus, Aeneides, Desmognathus*), both in

Europe and in America, the lungs, trachea, and larynx have entirely vanished, being represented by at most a depression on the floor of the oesophagus in the embryo, and even this may disappear in the adult. Intermediate stages in the degeneration occur in *Salamandrina* (Camerano, 893 ; Lühe, 917 ; Lönnberg, 1899). Respiration in these lungless Urodeles is carried out by the vascularised surface of the skin, the bucco-pharynx, and even the oesophagus (Bethge, 1898 ; Barrows, 1900). Considerable modifications are entailed in the vascular system, both pulmonary vein and left auricle being reduced (Bruner, 892).

In the Amniota not only is the trachea strengthened by cartilaginous rings, incomplete dorsally in the Reptiles, but from its hinder end are differentiated two extra-pulmonary bronchi of similar structure leading to the lungs. The glottis can be firmly shut in Reptiles and Birds, and is closed in Mammals by a protective flap supported by cartilage, the epiglottis. As the neck becomes differentiated and lengthened, so does the trachea elongate and the lungs retire to the thoracic region with the heart. Their inflation is brought about according to the principle of the suction pump, by the expansion of the thoracic chamber whose walls are (except in Chelonians, see p. 600) provided with well-developed jointed movable ribs articulating for the most part with the ventral sternum. Contraction of the intercostal muscles draw-ing forwards and straightening the ribs expands the thoracic cavity, and air rushes into the lungs through the open glottis.

FIG. 605.

Diagram of longitudinal section through lung of Lacertilian. *br*, Lateral external bronchus; *lbr*, lateral secondary bronchus leading to air-cells; *mbr*, main internal bronchus; *a*, anterior, and *p*, posterior saccular extensions of bronchi.

Relaxation of the muscles and the collapse of the ribs accompanies expiration. These respiratory movements are further helped by the development of septa and diaphragms (see below).

In the course of adaptational evolution, the lungs of the Amniota become more and more specialised in divergent directions. Starting from such a mere saccular enlargement as we find in Amphibia, with thin slightly folded walls enclosing a spacious central cavity, the distinction between the air-passages and the truly respiratory region becomes more pronounced, the latter being ever increased to afford a larger surface for respiratory exchange. Numerous and small alveoli, lined with the

thinnest epithelium, become set round internal chambers delimited by in-growing septa. These chambers become regularly disposed so as to lead out from a central cavity which grows more defined and tubular by the regular arrangement of the edges of the septa, until they finally surround intra-pulmonary passages or bronchi. The chambers themselves may be differentiated into mere air-passages leading from a bronchus to more numerous atria beset with alveoli. Thus gradually develops the spongy parenchyma of the higher types of lung, Figs. 605-606, 638.

Reptilia.—The minute structure of the lung in Reptiles has been studied of late by Miller and Milani (920). As a rule in Lacertilia and Ophidia the more parenchymatous part is situated in the anterior region near the entrance of the bronchus, and gradually dwindles towards the apex, which may be thin-walled and saccular. In the Varanidae, Crocodilia, and Chelonia, where the parenchyma is more developed, distinct secondary bronchi expanding into chambers radiate from a tubular meso-bronchus. Moreover, in the Chelonia and certain Lacertilia (Ascalobatae, Iguanidae, Varanidae) the terminal thin-walled sac may be prolonged into blind processes. These are especially well developed and numerous in Chamaeleons, where they extend among the abdominal viscera and help the animal to distend itself, Fig. 606. Probably as a consequence of the elongation of the body, snakes and snake-like lizards usually have a vestigial left and lengthened right lung.
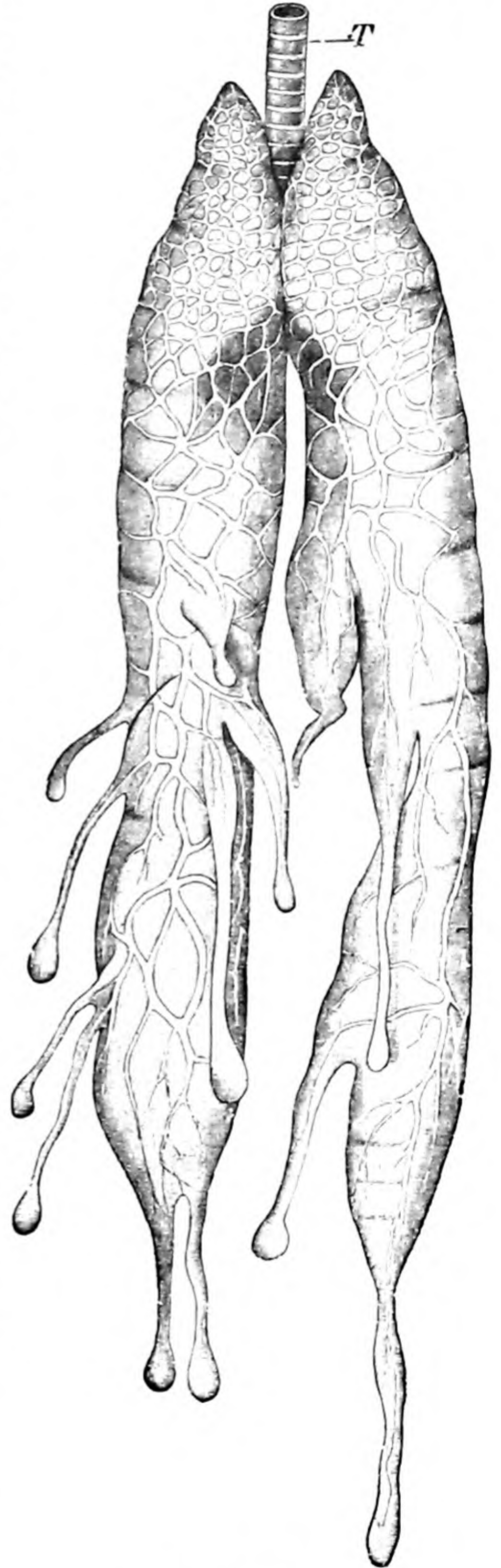
FIG. 606.

Lungs of *Chamaeleo monachus*. T, Trachea. (From Wiedersheim, *Comp. Anatomy*.)

Owing to the presence of a hard carapace and plastron, often rigidly connected together, respiration cannot be carried out in Chelonians as it is in other reptiles by means of the movable ribs. It is therefore brought about by a special mechanism peculiar to the Chelonian (Townson, 1799; Weir-Mitchell, 1870; P. Bert, 1870). Inflation and deflation of the lungs, highly differentiated organs closely adpressed to the carapace, is due to some extent to the drawing in and out of the neck and limbs, but chiefly to the action of the pectoral and pelvic limb girdles, whose remarkable position and attachments within the 'shell' allow a certain rotary movement (Sabatier, 1881; Charbonnel-Salle, 1883; François-Franck, 1906). The posterior oblique muscle and the post-hepatic septum help in the respiration of crocodiles (p. 641).

Aves.—Most interesting, however, is the respiratory apparatus of birds, whose body has to be kept at a constant high temperature, and whose great metabolic activity during violent muscular exertion has to be provided for. In the bird's lung, indeed, the respiratory exchange is probably more intense and more effectively carried out than in any other respiratory organ known, and the lungs become differentiated into what may be called the lungs proper, situated in the thoracic region close up against the ribs and vertebral column, and blind thin-walled distensible air-sacs extending among the viscera. Ever since Harvey, in 1651, proved that the apertures on the ventral surface of the lung lead into air-sacs, and Camper (1773) and Hunter (1774) further showed that these sacs lead into air-cavities in the bones, the breathing apparatus of birds has attracted the attention of a multitude of observers. But it is only quite recently that the peculiar structure of the avian lung has been fully appreciated. For our knowledge of the anatomy of the sacs we are chiefly indebted to the work of Sappey (1874), Campana (894), and Huxley (911); but much detail has been made known by Schulze (1871), Beddard (953), Guillot (904), Roché (936), Müller (923), Weldon (1883), Juillet (912), and others; while their development has been revealed by Selenka (1866), Bertelli (955), Poole (974), Juillet (912), Locy and Larsell (916). Briefly the air-sacs may be described as, so to speak, the blown-out extremities of certain bronchial tubes, Figs. 607-9. There are usually five pairs : a cervical extending up the neck; an interclavicular pair, usually fused to a median sac ventral to the oesophagus in the pectoral region (remaining separate in Vultures, *Ciconia*, and *Ardea*); an anterior and a posterior pair of thoracic or intermediate sacs, below the ribs and in front of the post-hepatic septum (p. 633); and lastly, two abdominal sacs, which push far into the abdominal cavity, except in *Apteryx* (Huxley, 911). Rarely there are three pairs of intermediate

sacs (*Podargus*, Beddard, 1898). These thin-walled non-vascular sacs become pressed against each other, the ventral surface of the lungs and the oblique septum (pp. 633, 639), and are permanently distended with air to a greater or less extent. Much speculation has arisen about their
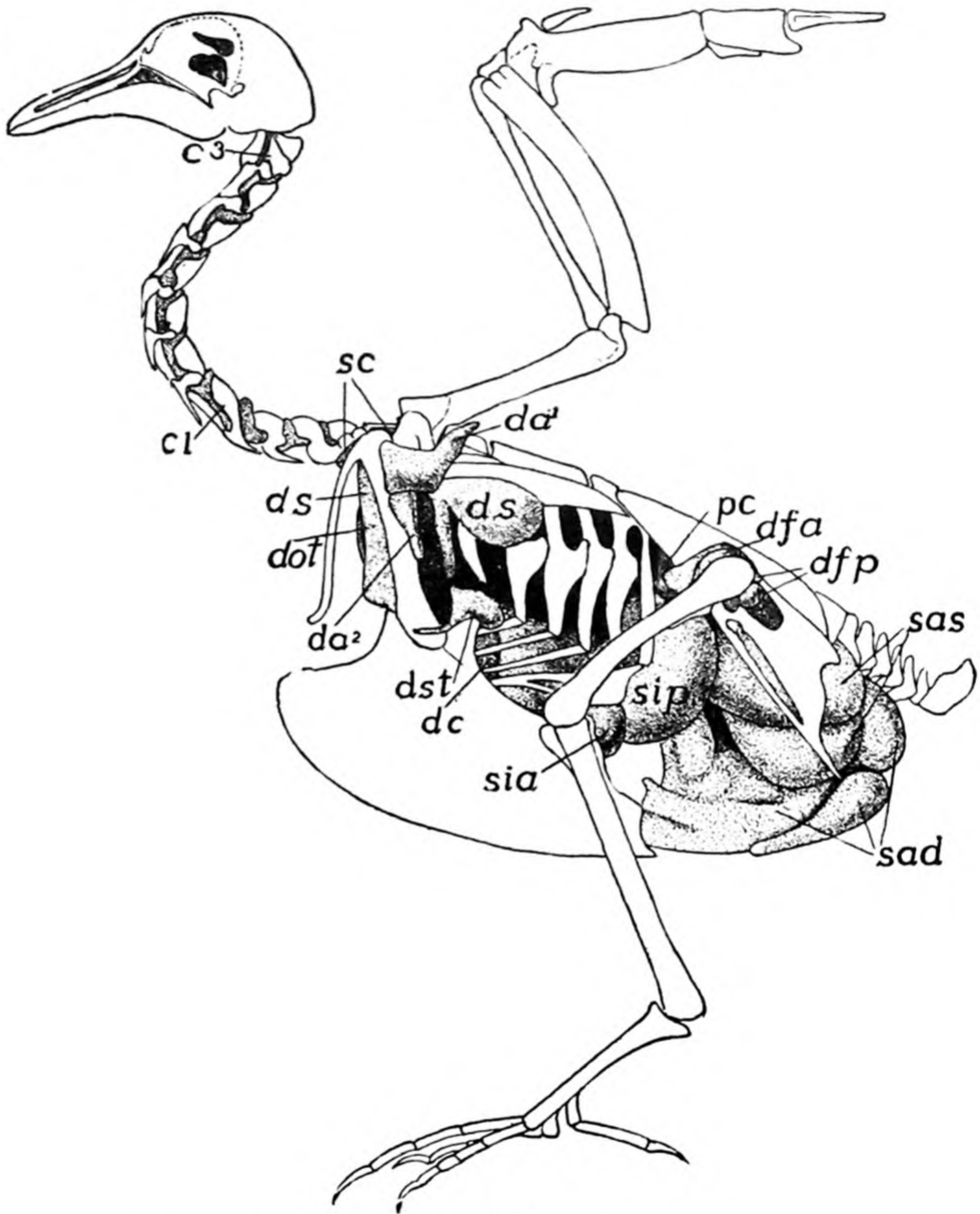
FIG. 607.

Air-sacs and canals leading into bones of pigeon (after B. Müller, from J. S. Kingsley, *Comp. Anat. of Vertebrates*, 1926). c^{1-3}, Intertransverse canals; da^{1-2}, axillary sac and its ventral diverticulum; *dc*, canal for ribs; *dot*, infraclavicular canal; *ds*, subscapular sac; *dst*, sternal canal; *pc*, pre-acetabular canal; *sad*, *sas*, right and left abdominal sacs; *sc*, cervical sac; *sia*, *sip*, anterior and posterior intermediate or thoracic sacs.

function. That their chief use is to help in respiration there can be no doubt (Harvey, 1651; Perrault, 1666; Sappey, 1847; Campana, 894). Placed between the skeleton above and an almost rigid sheet of connective

tissue below (pulmonary diaphragm of Sappey, pulmonary aponeurosis of Huxley, ornithic diaphragm of Bertelli), the lungs proper hardly alter at all in volume in breathing; they are relatively small and enclosed in virtual pleural cavities (p. 639). This arrangement is to some extent foreshadowed in the Crocodilia, where the lungs are also enclosed in pleural cavities distinct from the abdominal coelom (p. 641). The original lung has in fact become differentiated into two regions: the closely packed parenchymatous vascular lung in which respiratory exchange takes place, and the saccular diverticula whose function it is to serve as reservoirs for pumping air through it. Campana adopted the then prevalent theory that the intermediate sacs received most of the
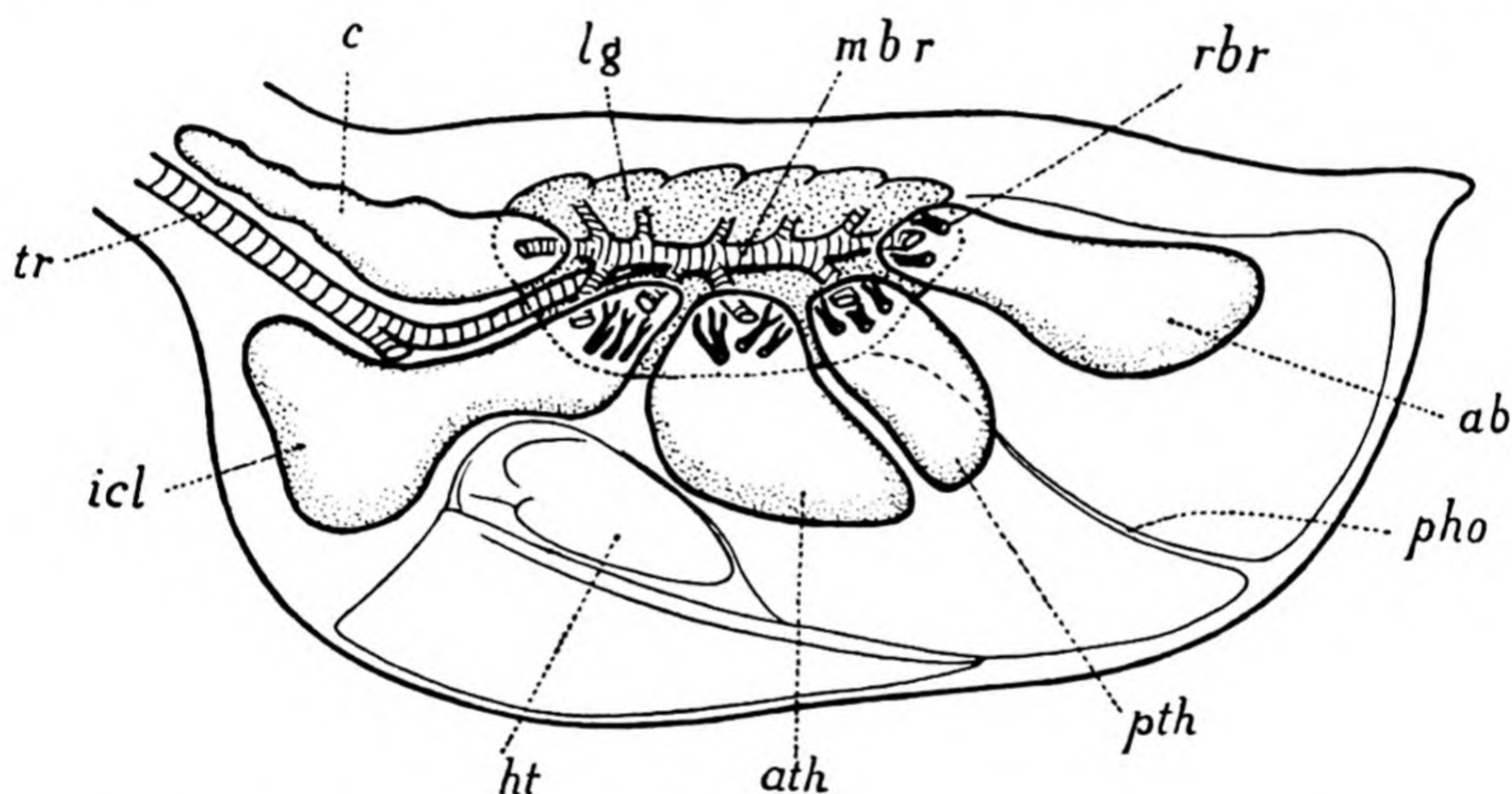
FIG. 608.

Diagram of respiratory organs of a Bird, left-side view. *ab*, Abdominal air-sac; *ath*, anterior thoracic air-sac; *c*, cervical air-sac; *ht*, heart; *icl*, interclavicular air-sac; *lg*, left lung; *mbr*, meso-bronchus; *pho*, post-hepatic septum; *pth*, posterior thoracic air-sac; *rbr*, recurrent bronchi; *tr*, trachea.

fresh air from the bronchi at inspiration, when the ribs are straightened and the sternum lowered; the more anterior and posterior sacs being filled from the intermediate sacs when the thorax contracts. The outer sacs would thus be expanded when the intermediate sacs are compressed, the small muscles of the pulmonary diaphragm serving to keep constant the volume of the lung at expiration. Thus by the alternate contraction of antagonistic sacs (Perrault, 1666) a constant flow of air would be kept without intermission through the lung at average tension and composition. Moreover, the large surface of the sacs serves to keep the air both warm and damp, and mixes the new air with the old. But this theory of antagonistic sacs has been considerably modified by later observers (P. Bert, 1870; Soum, 1896; Bär, 1896). To understand avian respira-
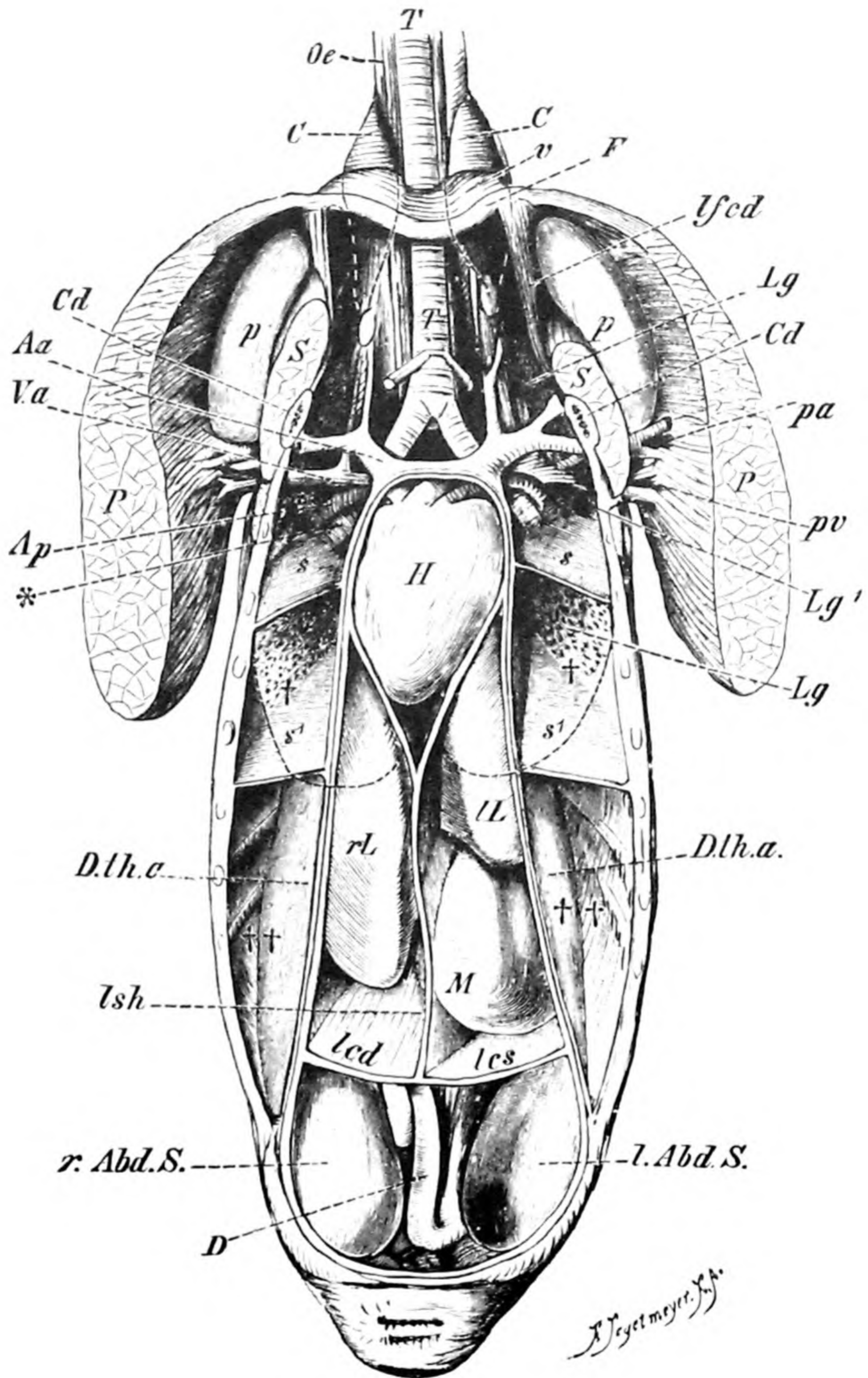
FIG. 609.

Abdominal viscera and air-sacs of a duck after the removal of the ventral body-wall. (From a drawing by H. Strasser.) *Aa, Va,* Innominate artery and vein with their branches; *Ap,* pulmonary artery; *C, C,* cervical sacs; *Cd,* coracoid; *D,* intestine; *D.th.a,* oblique septum; *F,* furcula; *H,* heart, enclosed within the pericardium; *lfcd,* coraco-furcular ligament; *Lg, Lg¹,* lung; *lsh,* suspensory (falciform) ligament; *lcd, lcs,* right and left parts of post-hepatic septum; *P,* pectoralis major; *p,* axillary sac lying between the coracoid, scapula, and the anterior ribs, and communicating with the sub-bronchial air-sac; *pa, pv,* pectoral artery and vein; *r.Abd.S, l.Abd.S,* right and left abdominal (posterior) air-sac; *rL, lL,* right and left lobes of liver: *S,* subclavius muscle; *s, s,* partition walls between the anterior thoracic air-sacs and the unpaired sub-bronchial sac, lying in the anterior part of the body-cavity; *s¹, s¹,* partition walls between the anterior and posterior thoracic air-sacs; *T,* trachea; *v,* portion of anterior wall of the body-cavity; *,* point of entrance of the bronchi into the lung; †, anterior thoracic air-sac; ††, posterior thoracic air-sac.

tion we must now describe the recurrent bronchi discovered by Campana (894), but the full significance of which was first made known by Juillet (912), Figs. 608, 612, 636-7. The main or meso-bronchus passes down to open into the abdominal sac, and gives off lateral secondary branches to each of the other sacs. In the case of the cervical sac, the simple bronchial orifice on the surface of the lung proper, the large primary ostium, is the only communication ; but each of the remaining four sacs has in addition, as a rule, a group of small secondary openings leading back from the sac into recurrent bronchi which penetrate and branch in the substance of the lung ; and it is by means of these that relatively pure air received
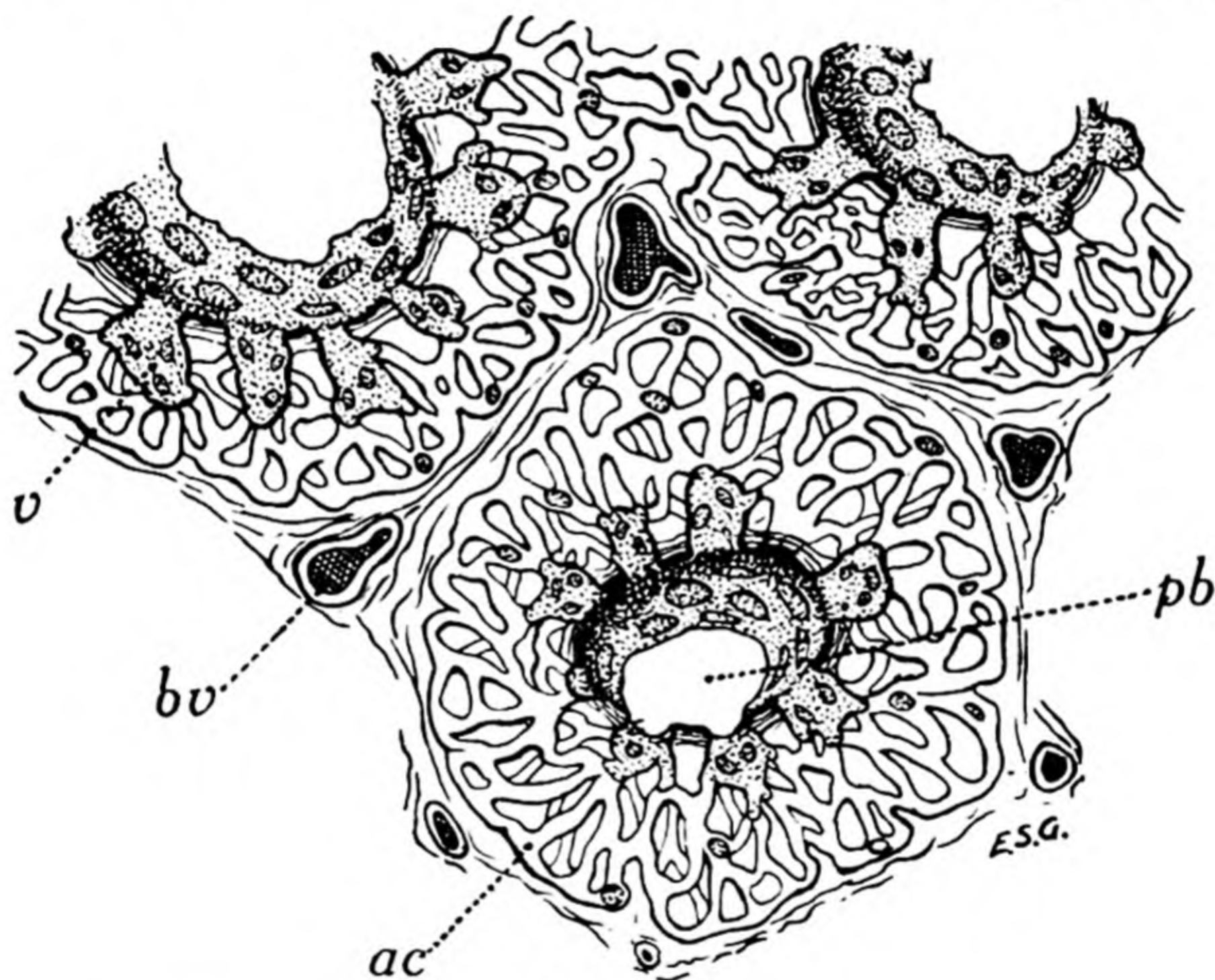
FIG. 610.

Diagram of a thick section of small portion of lung of a bird, much enlarged. *ac*, Air-capillaries with blood spaces between them ; *bv*, large blood-vessels ; *pb*, parabronchial cut across; *v*, vestibule, diverticulum into which open air-capillaries.

directly from the primary bronchus is returned to the lung from the sac, ensuring a thorough ventilation of the parenchyma.[1] During flight the interclavicular and anterior intermediate sacs would be specially active, being much influenced by the muscles of the wing ; but when at rest and when walking the posterior and abdominal sacs would be more effective. The mechanism regulating the flow of air from the sac back to the lung through the recurrent openings and not through the ostia into the large bronchi has not yet been satisfactorily elucidated. Probably

[1] No doubt when the avian lung was evolved from the reptilian, the constriction between the true lung and the air-sacs took place in such a way as to leave a few of the air-pockets on the side of the sac, and it is these distal diverticula which became converted into the recurrent bronchi.

muscular contraction of the ostia and valvular folds contributes to this end ; but the evidence of observers on this point is contradictory.

The lung itself has become marvellously adapted to secure the greatest possible surface for respiratory exchange and the most perfect ventilation of its parenchyma. It is chiefly to the later work of Fischer (899), Juillet (912), Locy and Larsell (916), and Larsell (915), that we are indebted for the elucidation of the unique structure of the bird's lung, which differs from that of all other vertebrates in that it contains no culs-de-sac, no blind air-cells, but only freely communicating anastomosing passages forming complete air-circuits. As already explained, the extra-pulmonary bronchus enters the lung and passes down to its hinder end as the main bronchus, giving off as a rule four large secondary ventral bronchi, and then eight secondary dorsal bronchi; to these may be applied Huxley's terms, mesobronchus, entobronchus, and ectobronchus respectively. There are, in addition to these, six laterobronchi and some dorsobronchi. These various secondary bronchi soon branch into tertiary parabronchial tubes of uniform bore which join end to end with those of neighbouring bronchi and of the recurrent bronchi. Further, as shown by Rainey and Williams
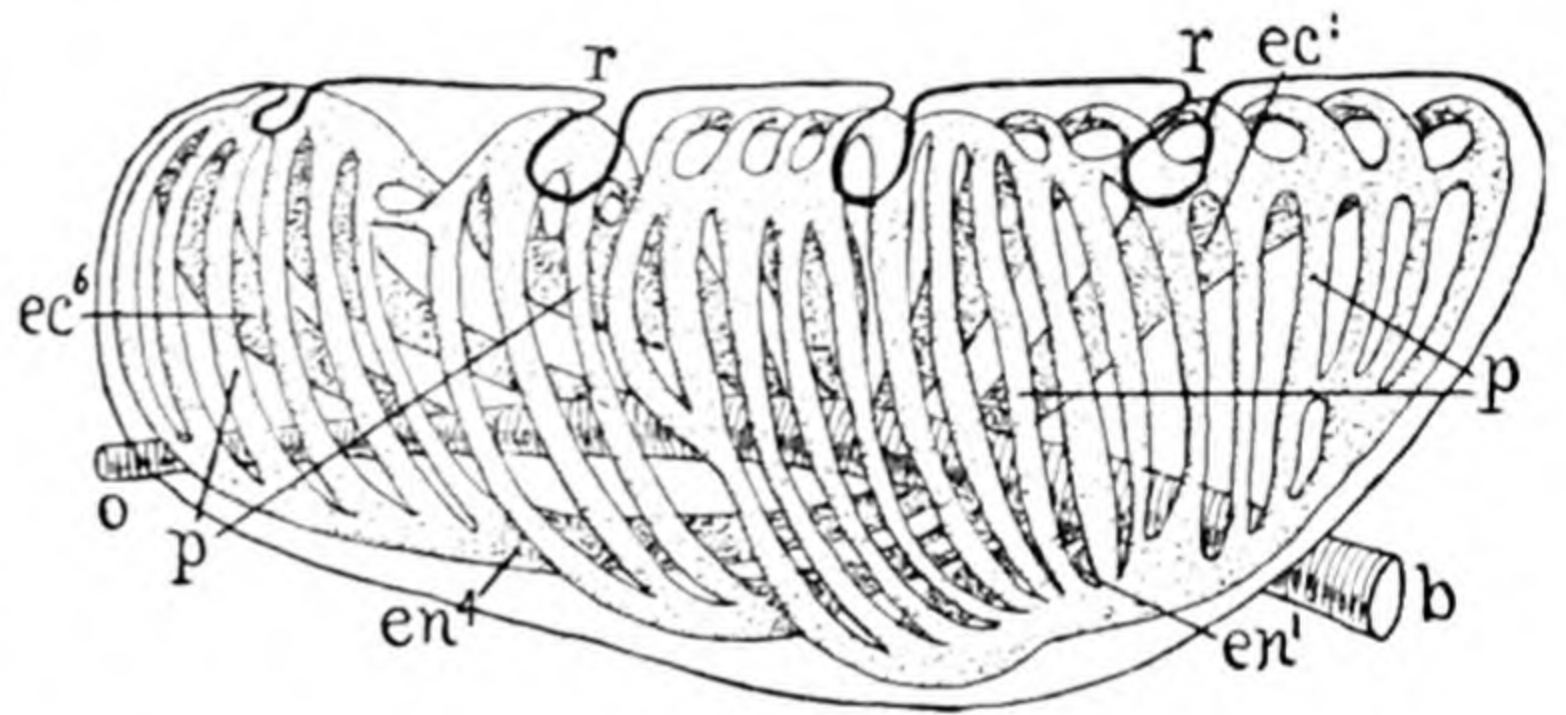
FIG. 611.

Diagrammatic side view of right lung of bird showing parabronchi connecting ecto- and endobronchi (after Locy and Larsell, from J. S. Kingsley, *Comp. Anat. of Vertebrates*, 1926). *b*, Bronchus ; *ec*, ectobronchus ; *en*, endobronchus ; *o*, opening into abdominal sac ; *p*, parabronchus ; *r*, impression of ribs.

(1859), the parenchyma without air-cells consists of hexagonal areas surrounding the parabronchi, supplied by blood-vessels, and pierced by a system of air-capillaries (Fischer, 899), offshoots from the parabronchi forming an anastomosing network of minute air-circuits leading from one parabronchus to another, and from recurrent to excurrent parabronchi. The spongy mass of the lung thus consists of a complex network of interlacing blood-vascular and air-capillaries of great efficiency, Fig. 610.

The fact that the bones of birds often contain air instead of marrow is said to have been first mentioned by the Emperor Frederick II. in a treatise on the chase in the thirteenth century. This pneumaticity, due to the penetration of diverticula from the sacs, varies greatly in extent. Although generally well developed in good fliers, this is by no means always the case, since it is absent in gulls and little developed in small birds. Every gradation is known, from that of the Penguins in which

no bones are pneumatic to that of the Frigate bird in which they all are down to the metatarsals. The early fossil birds *Archaeopteryx* and *Hesperornis* seem not to have possessed pneumatic bones (Marsh); but the vertebrae of some Dinosaurs were pneumatic. It is the cervical sac which supplies air to the cervical and thoracic vertebrae and ribs, the interclavicular to the pectoral girdle wing sternum and sternal ribs, and the abdominal to the hinder parts of the skeleton (Campana, 894). More or less extensive diverticula may also spread underneath the skin and among the muscles, especially in good fliers and aquatic birds.
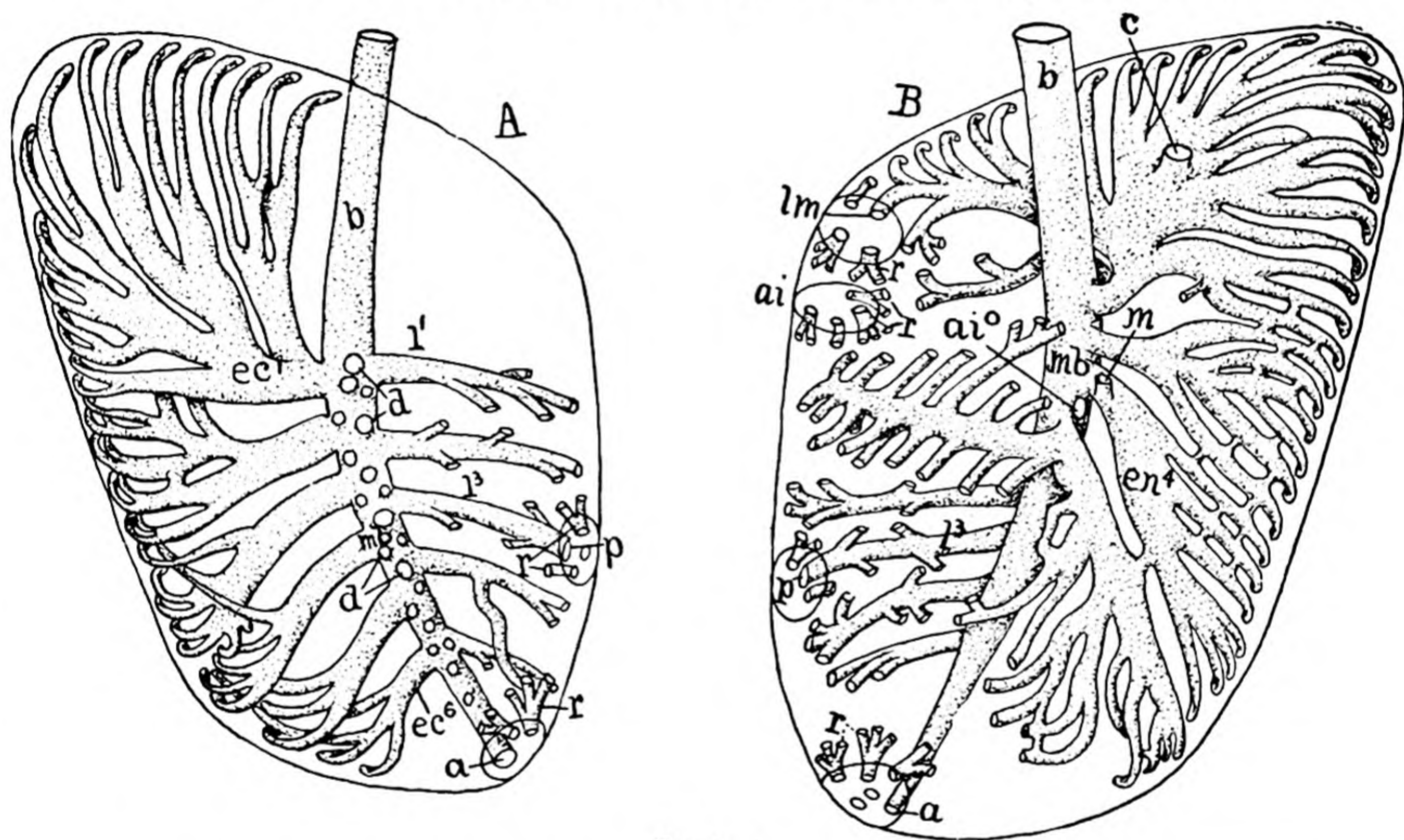
FIG. 612.

Diagrams of lung of hen, *Gallus domesticus* : A, Dorsal, B. ventral aspect (after Locy and Larsell, from J. S. Kingsley, *Comp. Anat. of Vertebrates*, 1926). *a*, Opening of mesobronchus, *mb*, into abdominal air-sac ; *ai*, region of recurrent bronchi from anterior intermediate sac ; *ai⁰*, opening of *b*, bronchus, into intermediate sac ; *c*, opening into cervical sac ; *d*, roots of dorsibronchi ; *ec*, ecto-bronchi ; *en*, entobronchi ; *l*, laterobronchi ; *lm, m*, openings into lateral and medial moieties of inter-clavicular sac ; *p*, opening into posterior intermediate sac ; *r*, recurrent bronchi from abdominal sac.

The development of the lungs and air-sacs takes place as follows. Starting from the paired evaginations already mentioned, the lung rudiments join a median tracheo-laryngeal groove which is constricted off from the oesophagus. The paired endodermal diverticula grow backwards, surrounded by a thick layer of mesenchyme covered with coelomic epithelium ; soon they bud off side branches which, penetrating the mesenchyme, give rise to the secondary bronchi we have described in the adult, while the main stem becomes the mesobronchus. Numerous parabronchi now budding·off from the secondary bronchi fuse end to end with and open into branches from other bronchi. Still more numerous

and finer outgrowths anastomose and complete the system of air-capillaries, thus establishing the characteristic air-circuits. Meanwhile the air-sacs grow out from the surface of the young lung as paired rudiments or buds. The cervical sac arises from the first entobronchus, the anterior intermediate sac from the third entobronchus, the posterior intermediate from the third laterobronchus, the abdominal sac from the extremity of the mesobronchus. The interclavicular sac has a double rudiment on each side, one from the first entobronchus and the other and larger from the third entobronchus ; these two fuse not only with each other, but also in most birds with the corresponding sac of the opposite side. In the meantime the recurrent bronchi have budded off from the necks of the developing sacs, and grow inwards to branch and finally anastomose with the other parabronchi, Figs. 633-7.

What can be the function of these extensive air-cavities, besides that already discussed of acting as accessory respiratory reservoirs to ensure a continuous instead of an intermittent flow of air, has long puzzled zoologists. That, being filled with warm air, they may serve as aerostatic organs was long ago suggested ; but Campana has conclusively proved that their lifting power is quite negligible. They may lower the specific gravity of a bird's body by 4 per cent at most. The replacement of marrow by air in the skeleton lessens the absolute weight ; but here again the difference is probably insignificant, and far surpassed by the variation in the relative weight of the skeleton in different species, and by the difference in weight due, for instance, to the taking in of food even at a single meal. In floating and diving birds, however, the air-cavities act as hydrostatic organs, also in singing birds as reservoirs of air, and generally they may serve to distribute the weight and so help to shift the centre of gravity to an advantageous point in flight. On the whole, the respiratory function seems to be by far the most important.[1]

Mammalia.—Although the differentiation of the lung has taken place in Mammals on the same principle, so to speak, as in Reptiles and Birds of increasing to the greatest possible extent the respiratory surface, yet the mammalian lung has been doubtless evolved along independent lines, and to trace its development we should probably turn back to the un-

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[1] Another possible function (Campana, Vesiovi, Madarasz) is that or lowering the temperature by offering a large surface for evaporation. Since birds do not sweat and are covered with a non-conducting layer of feathers, they must have some way of keeping down their temperature during violent exertion. Indeed, the whole question of the mechanism for heat regulation in birds seems not yet to have been adequately worked out. It must differ radically from that of mammals, has been independently acquired, and would doubtless well repay investigation.

differentiated type of the Amphibian or lower Reptile such as *Sphenodon,*
Intermediate steps are lacking, since even the Monotremes are thoroughly
mammalian in their respiratory apparatus.

The lung of the mammal is characterised by the great development
of a branching tree-like system of intra-pulmonary bronchi. These
ramifying tubes, whose walls are strengthened by cartilages, are
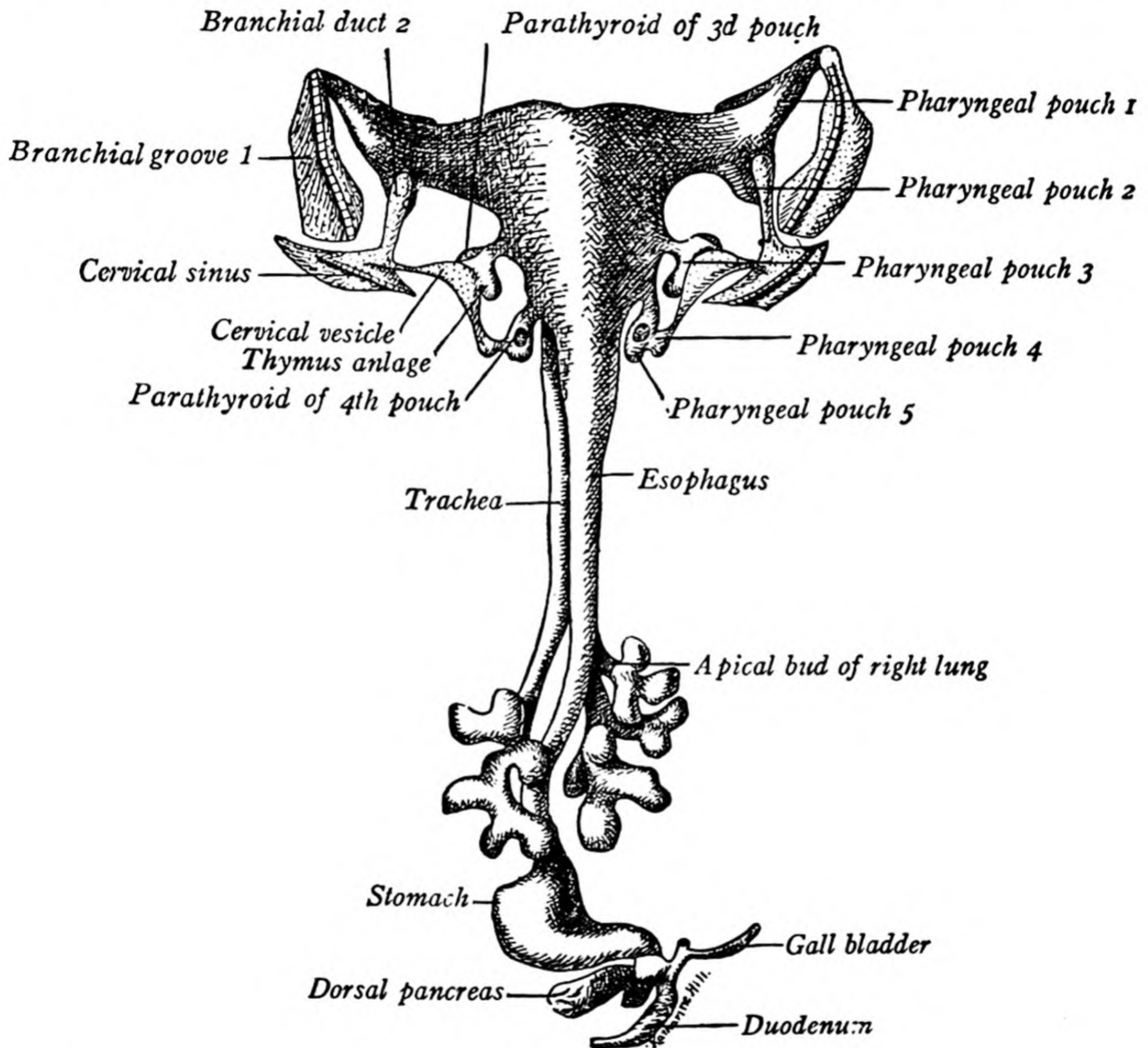
FIG. 613.

A reconstruction of pharynx and fore-gut of 11·7 mm. human embryo seen in dorsal view (after Hammar). Ectodermal structures are stippled. (From Prentiss and Arey, *Text-book of Embryology,* 1917.)

provided with a layer of smooth muscle fibres, and a lining of columnar
ciliated epithelium reaching as far as the slender bronchioli entering the
lobules. The latter are separated from each other by connective tissue,
and in each of them the bronchiolus branches into respiratory bronchioli
leading to alveolar ducts which expand into atria. Finally the atrium,
and the infundibula or alveolar saccules coming from it, are beset with

minute alveoli or air-cells. Alveolar duct, atrium, saccule, and alveolus are all lined with a very thin flat epithelium, covered externally by a close network of capillaries. It is in this region that the respiratory exchange takes place (Oppel, 795).

Aeby (883) was among the first to make a detailed systematic study of the bronchial tree, and to point out that in the vast majority of mammals it is built on a remarkably asymmetrical plan. From each stem bronchus arise secondary bronchi : a main outer lateral series (called ventral by Aeby and many authors since, but more correctly named lateral by Robinson, 935) ; a dorsal series and a less complete ventral series (called accessory by Aeby, and supposed by him to be secondarily derived from the lateral). There may also be present a less developed and less regular series of internal lateral bronchi (d'Hardiviller, 908 ; Flint, 900).
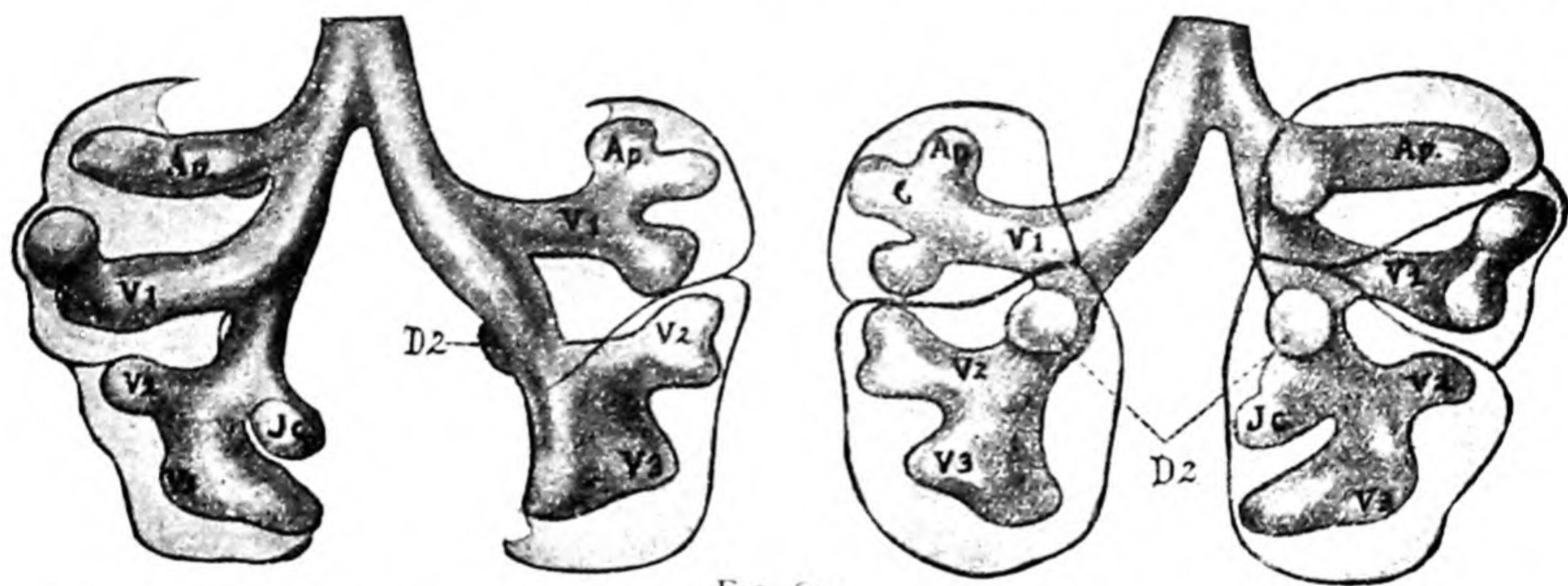
FIG. 614.

Ventral and dorsal views of lungs from human embryo of about 9 mm. (after Merkel, '02) (from Prentiss and Avey, *Text-book of Embryology*, 1917). *Ap*, Apical bronchus ; *D1, D2*, etc., dorsal, *V1, V2*, etc., ventral bronchi ; *Jc*, infracardial bronchus.

These secondary bronchi are given off at fairly regular intervals along the stem bronchus, and diminish in size from before backwards to the tip of the tree. The dorsal and ventral series correspond in position, but alternate with the lateral. The pulmonary vein enters the lung ventrally and branches, spreading over the ventral surface of the bronchi. On the contrary, the pulmonary artery, although likewise entering from below, passes round the outer side of the stem bronchus, runs back along its latero-dorsal surface, and spreads over the more dorsal aspect of the bronchial tree. Now Aeby, who held that the artery exerts a controlling influence over the distribution of the bronchi, pointed out that, whereas in the left lung not only the ventral regions, but also the anterior apex, are supplied by the lateral series coming off below the artery, and therefore termed hyparterial ; in the right lung the apical region is supplied by a distinct bronchus coming off more dorsally, passing above the artery, and termed eparterial, Figs. 613-14, 648. The asymmetry is further marked

by the great extension of the first of the ventral bronchi on the right side to supply the infra-cardiac lobe, large in most mammals, but reduced in some, as in man. This lobe is developed in a special diverticulum of the right pleural cavity situated between the diaphragm and the heart, Figs. 644-5, 654.

Much controversy has taken place about the significance of the eparterial bronchus. With few exceptions it occurs on the right side in all species not only of the Placentalia but also of the Marsupialia and Monotremata (Aeby, 883; Huntington, 910; Narath, 924-5). The known exceptions are certain genera in which it occurs on both sides, such as *Bradypus*, *Phoca*, *Equus*, *Auchenia*, *Elephas*, *Phocaena*, *Delphinus*, and *Cebus*; and *Hystrix* and *Taxidea*, in which it does not occur at all. In the Artiodactyle Ungulates and the Cetacea it may arise from the trachea; sometimes its origin is bronchial on the left and tracheal on the right (*Auchenia*, *Delphinus*). Aeby concluded that the eparterial is a special bronchus not usually represented on the left side, and therefore that the apical lobes of the two lungs are not truly homologous.

Narath, whose results have been generally accepted, strongly opposes Aeby's conclusions, denies, like Zumstein before him, the importance of the position of the pulmonary artery, and maintains that the eparterial bronchus is merely the specialised first bronchus of a dorsal series, and that it is still, where apparently absent, attached to the first ventral bronchus, of which it is probably the dorsal branch as suggested by Willach.

Moreover, Narath holds that the dorsal series of bronchi are phylogenetically to be derived from the lateral bronchi, of which they are to be considered as branches which have migrated on to the stem bronchi; and the same suggestion is made about the ventral series. Development, however, does not support this view, as it seems clearly established that the series of secondary bronchi appear regularly on the stem bronchi from before backwards as independent buds (Flint, in the pig; E.S.G., in *Trichosurus* and the mouse). Moreover, it seems far more probable that the arrangement of the secondary bronchi in three or four series is derived from the reptilian condition, where the outgrowths are more numerous and less regular, by their reduction and specialisation. Huntington, extending Aeby's observations on the adult tree, concluded that the symmetrical bilateral hyparterial type (*Hystrix*, *Taxidea*) is the most primitive, leading through the type with a right eparterial to the symmetrical eparterial type (*Cebus*, *Phoca*, etc.). But this theory cannot seriously be maintained. The exceptional cases in which there appear to be two eparterial bronchi are sporadically distributed among the higher

mammals, and are possibly due to the functional replacement of the original eparterial by the next pair of dorsal bronchi. Observations on the development of these mammals are greatly needed. The two forms without eparterial bronchus (*Hystrix*, *Taxidea*) possess lungs of very aberrant structure. On the other hand, the asymmetrical type is widely prevalent, fully developed in the most primitive groups, and appears in the very earliest stages in the ontogeny of the bronchi, not only of the Ditrematous but also of the Monotrematous mammals (*Echidna*, Narath, 924 ; *Ornithorhynchus*, E.S.G.). There can be little doubt that this type was established in the primitive ancestral mammal.

It is generally supposed that the asymmetry of the bronchi is an adaptation to allow for the backward motion of the heart and the development of the left aortic arch, leading either to the suppression of the eparterial bronchus on the left (Aeby), or to its non-separation from the first lateral (Willach, Narath). However, no trace of a left eparterial bronchus has been discovered in the embryo by most authors ; although d'Hardiviller described in an early stage of the rabbit a left eparterial, which vanishes later, and Bremer (890) observed the same in the embryo of the opossum, *Didelphys*. These observations need confirmation, and it seems not improbable that these authors described either abnormalities, or a first dorsal for the true eparterial bronchus. If we are unable to accept the view of Willach and Narath that the eparterial is homologous with the apical branch of the first left lateral, since there is no evidence that a bronchus can migrate from a hyparterial to an eparterial position, we may still hold that it is essentially merely the first of the dorsal series.

General Development and Phylogeny.—Turning now to the more general significance of the mode of development of the lung structure, we find that new light has been thrown on this problem by the researches of F. Moser (921), confirmed on Reptiles by Hesser (909). She holds that the subdivision of the lumen of the lung is brought about in ontogeny, not by the formation of ingrowing septa, but by the outgrowth of successive bud-like branches from a primitive mesobronchus in the lower as well as in the higher forms. The buds penetrate, sprout, and expand in the surrounding mesoblastic tissue, and thus the thicker this layer of mesenchyme the deeper will be the cavities and the more developed will be the walls separating them. The Amphibian lung-rudiment having but little mesenchyme, the central lumen is large and the peripheral chambers shallow; moreover, the buds are irregularly distributed. On the other hand, in the Amniota the mesenchyme is progressively increased, and the primary buds fewer and more regular in their origin, but more subdivided distally, leading to the

mode of development so admirably described by numerous observers in Mammals (His, Narath, Flint, etc.). We have already sketched this development in the case of the bird (p. 606). There remains only to mention the long controversy held as to whether, especially in the Mammalia, the ramification of the embryonic bronchus takes place according to a monopodial or a dichotomous plan (in the latter case by subdivision of the growing tip, in the former by lateral sprouting from the main stem). Most of the older authors (Remak, Koelliker), and more recently Ewart (1889), Minot (1892), Justesen (913), interpreted the growth as dichotomous; but v. Baer, Cadiat, Küttner, Aeby (883), on the contrary, held it to be monopodial. Some have maintained that both processes take place (Robinson, 935; d'Hardiviller, 1897; Flint, 900). The work of Moser, Narath, and Flint may be considered to have established that the monopodial is the chief, if not the only mode of branching in early stages, that the buds grow out regularly in succession from the base of the bronchus to near its blind end, and that the main buds appear just short of the growing tip, except perhaps in the case of accessory bronchi. In later stages and towards the extremity of the finer twigs it is probable that monopody merges into dichotomy. Obviously intermediate stages between monopody and dichotomy may occur.

Although this may well be a correct account of the embryonic development of the lung, there can be little doubt that it cannot represent its phylogenetic history. Indeed, the lung seems to present a remarkably clear case of an ontogeny which is not recapitulative. For the accumulation of a thick layer of mesenchyme round the narrow endodermal rudiment of thick columnar epithelium can surely in no way repeat a primitive stage, but is rather due to the precocious gathering together of the building material for future differentiation. On the contrary, the lung, to be an efficient organ of respiration, must from the first have had a thin wall abundantly supplied with a superficial network of blood-vessels, and have become progressively folded and pocketed to form the parenchyma of air-cells in higher forms. Thus the respiratory surface, which is the last to develop in the embryo, must have been present from the first and throughout phylogeny, although doubtless less perfected in the lower than in the higher terrestrial vertebrates.

CHAPTER XII

SUBDIVISIONS OF THE COELOM, AND DIAPHRAGM

THE SUBDIVISIONS OF THE COELOM. THE PERICARDIAL COELOM AND SEPTUM TRANSVERSUM

IN the Craniata the coelom always becomes transversely subdivided more or less completely into separate chambers fulfilling special functions. The most constant of these, and the first to appear in both phylogeny and ontogeny, is the pericardial chamber, Fig. 615. Surrounding the heart below the fore-gut, it becomes completely shut off from the more posterior trunk coelom in all adult Craniates, excepting the Selachii, Chondrostei, and certain Cyclostomes (see below, p. 619). The pericardium in fishes is situated far forward, below and behind the posterior gill-arches. Its sides are formed by the body-wall; behind it is closed off by a firm, nearly vertical, septum transversum (see p. 616). It is protected above by the basi-branchials, and below by the pectoral girdle. Passing to the

Tetrapods we find that the pericardium moves farther and farther backwards away from the gill-arches; its side walls become thinner, being freed from the body-wall, and the thin septum transversum takes up an oblique position from before backwards and above downwards. This change, only begun in the Amphibia, accompanies the differentiation of a well-defined neck in the Amniota, and the retreat of the heart into the thoracic region above the protecting sternum. The backward migration of the heart and pericardium is always repeated in ontogeny. Meanwhile the pericardium tends to become more and more overlapped by the pleural divisions of the coelom, into which grow the lungs. Moreover, in the Sauropsida it becomes separated from the body-wall at the sides by the peritoneal coelom and liver, and in the Mammalia by the ventral
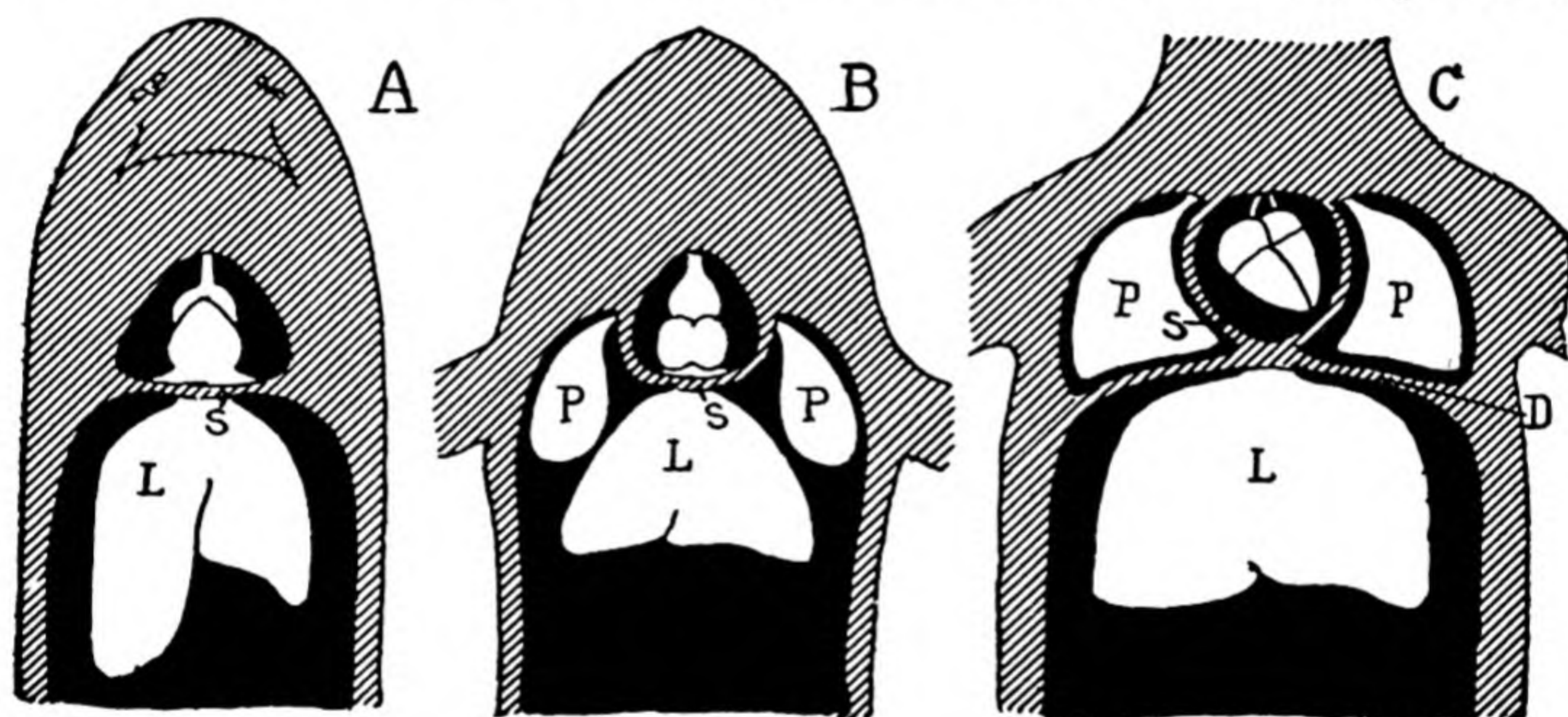
FIG. 615.

Diagram showing relations of coelomic cavities (black) in: A, Pisces; B, Amphibia and some Reptilia; C, Mammalia. (From J. S. Kingsley, *Comp. Anat. of Vertebrates*, 1926.)   L, Liver; P, lung; S, septum transversum; D, diaphragm.

extensions of the pleural cavities, which in man, for instance, leave the pericardium attached below only in the middle line above the sternum.

The function of the pericardial chamber is no doubt manifold and has changed somewhat from its first appearance in the lowest Craniata. Primarily it affords protection to the heart from surrounding pressures, and a free space filled with fluid in which the heart can easily undergo contraction. The stiffness of its wall in Pisces must also serve to maintain a negative pressure helping the venous flow back to the sinus venosus (see further, p. 536).

The closing off of the pericardial coelom takes place in very much the same way in the embryo of all Gnathostomes. In early stages the coelom of the lateral mesoblastic plate extends on either side of the median mesentery from the trunk into the pericardial region. The rudiment of the heart or ventral splanchnic vein below the oesophagus receives blood from the yolk-laden mid-gut by paired omphalomesenteric veins; but as

yet has no direct connexion with the somatic veins. Soon, however, the splanchnic wall, bulged outward by the omphalomesenteric veins, meets
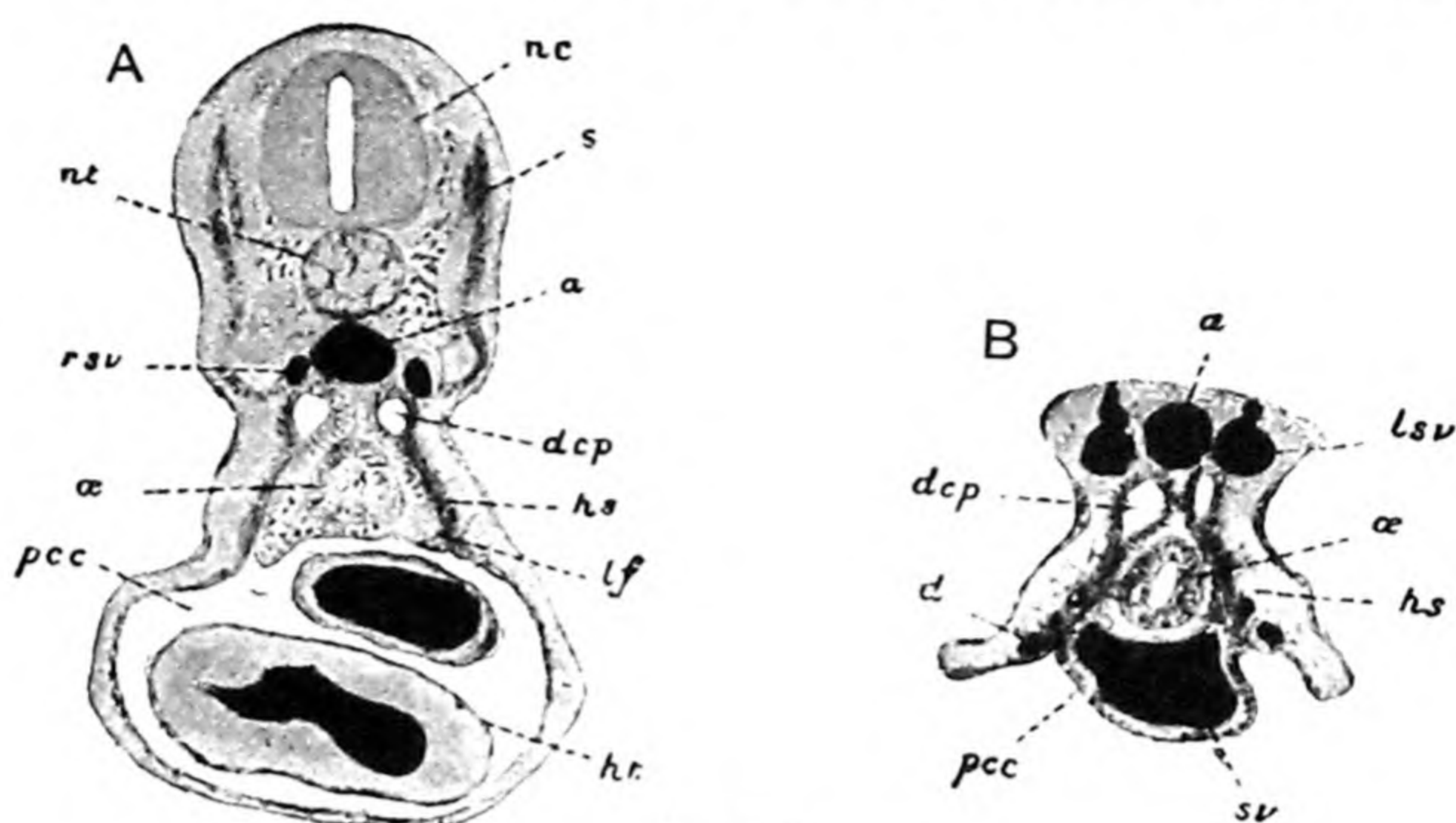
FIG. 616.

Transverse section of an embryo *Scyllium canicula*, Stage I, in A, posterior pericardial region, and B, region of sinus venosus; showing origin of horizontal septum or mesocardia lateralia, *hs*, by fusion of somatic and splanchnic walls leaving two dorsal coelomic passages above, *dcp*, and pericardial coelom below, *pcc*. *a*, Dorsal aorta; *d*, somatic rudiment of ductus Cuvieri; *ht*, heart; *lf*, lateral mesenterial fold; *lsv, rsv*, left and right somatic veins (future cardinals); *nc*, nerve cord; *nt*, notochord; *oe*, oesophagus; *s*, somite; *sv*, sinus venosus. (Figs. 616-19 and 621 from E. S. Goodrich, *Jour. of Anat.*, 1918.)

the somatic wall, and a bridge becomes established across the coelom on either side in which develop the ductus Cuvieri carrying blood from the
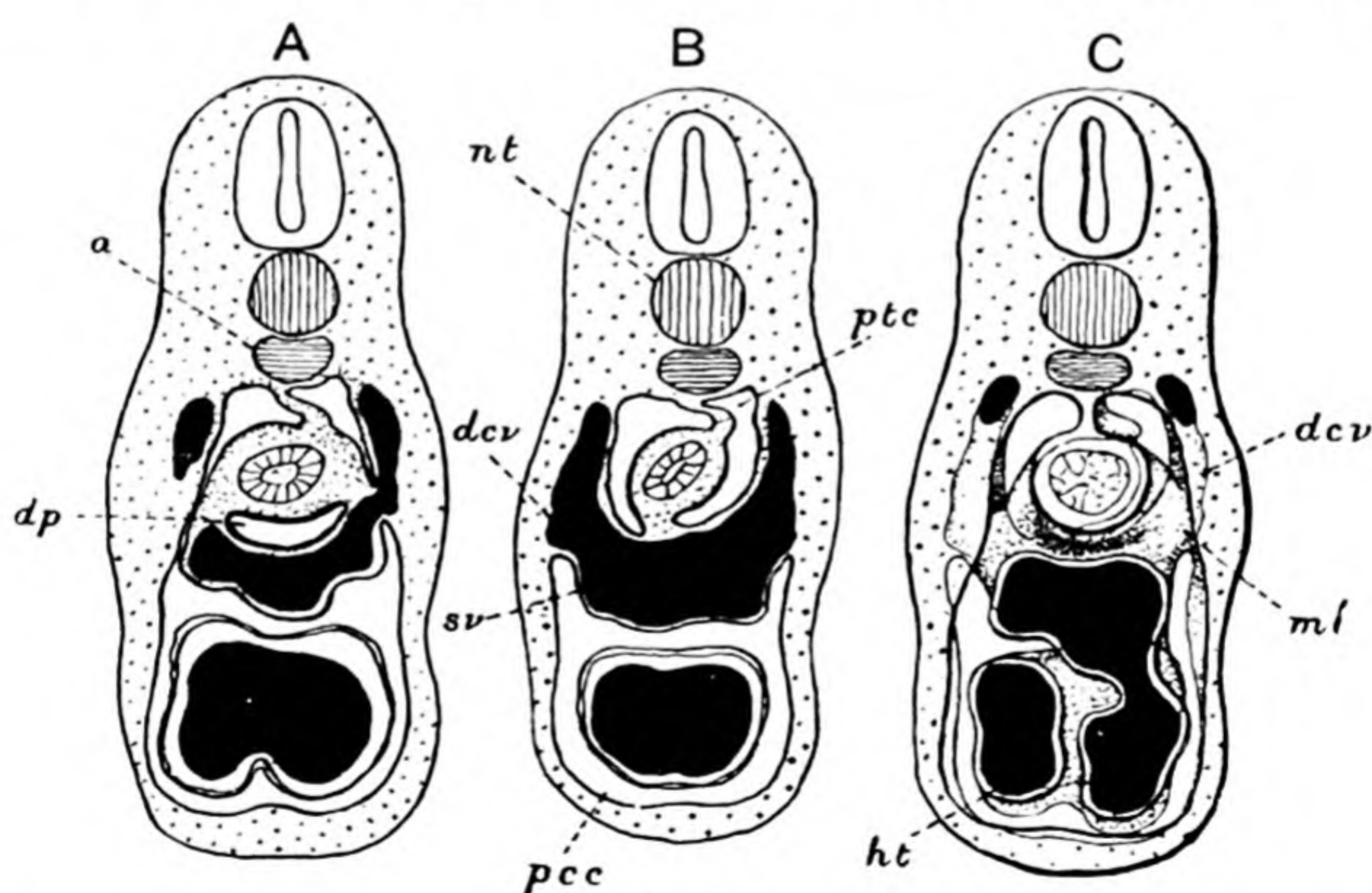
FIG. 617.

Embryo *Scyllium canicula*, Stage L. Transverse sections viewed from in front. A, Section through the median pericardial depression, *dp*, between the two lateral mesenterial folds; B, section farther back through the mesocardia lateralia and ductus Cuvieri; C, reconstructed thick section of same region, beginning in front of that drawn in A. *dcv*, Ductus Cuvieri; *ml*, mesocardium laterale; *ptc*, pericardio-peritoneal canal. Other letters as in Fig. 616.

somatic cardinal veins to that anterior part of the splanchnic vein destined to form the sinus venosus, Figs. 616-17. Thus arise the

'mesocardia lateralia' of Koelliker enclosing the ductus Cuvieri, and separating two dorsal and two ventral openings. On either side of the median mesentery is thus established a dorsal pericardio-peritoneal or pleuro-pericardial passage (recessus parietalis dorsalis of His), and a ventral pericardiaco-peritoneal passage (recessus parietalis ventralis). Into the anterior region of the ventral mesentery below the sinus venosus now grow the hepatic diverticula (see pp. 620-22), which soon by repeated branching subdivide the veins and develop into a bulky liver. Over the front face of this organ spreads the connective tissue of the mesentery to
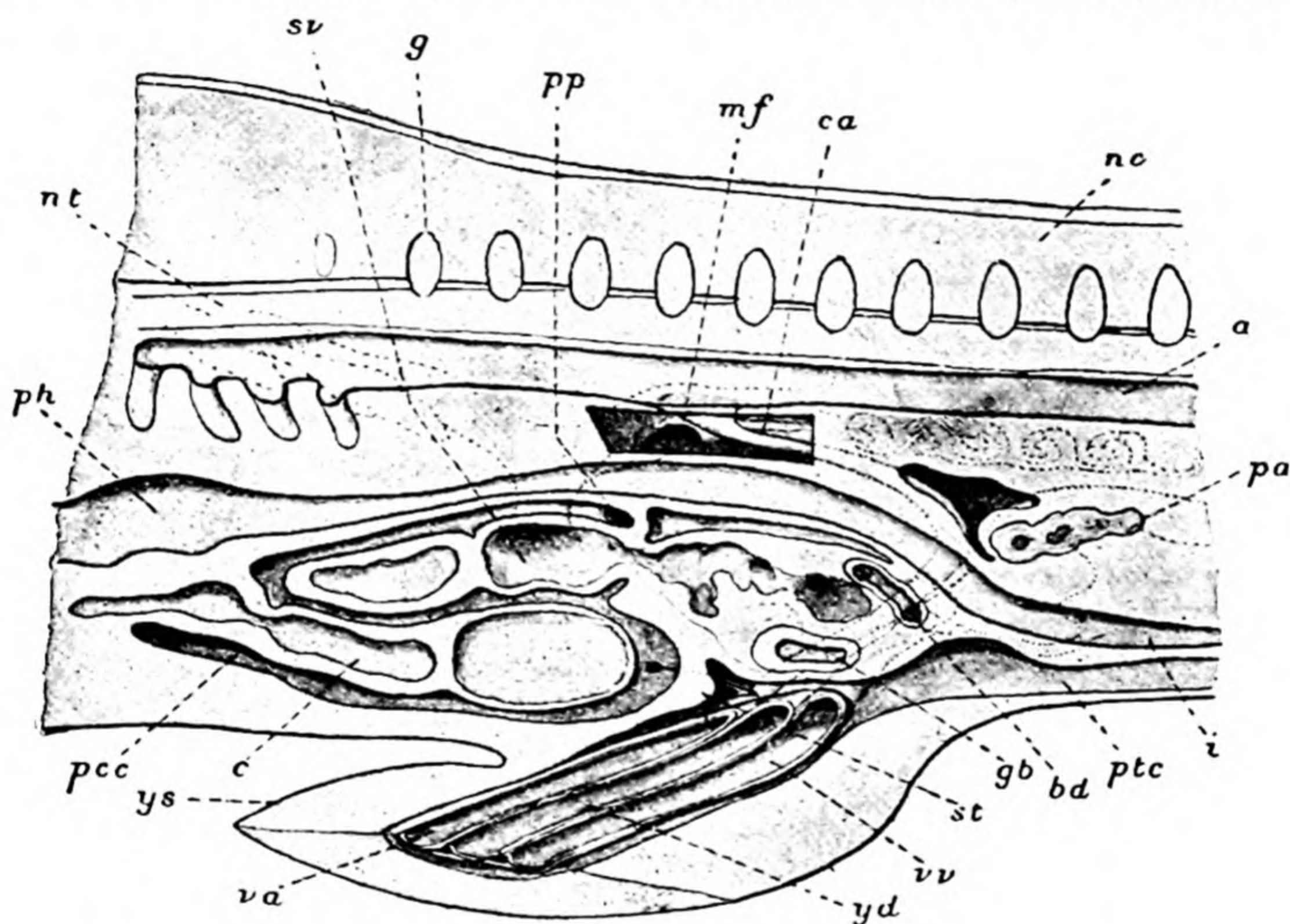
FIG. 618.

Inner view of right half of pericardial region of an embryo *Scyllium canicula*, 26 mm. long, reconstructed. Section cut to left of median mesentery through which a window has been cut to expose Müllerian funnel, *mf*, and the root of vitelline artery, *ca*. Behind pericardio-peritoneal opening, *pp*, is seen beginning of left mesenterial fold. An arrow passes behind mesohepatic ligament from pericardial to peritoneal cavity. *a*, Dorsal aorta; *bd*, bile-duct; *c*, conus; *g*, spinal ganglion; *gb*, gall-bladder; *i*, intestine; *pa*, pancreas; *ph*, pharynx; *st*, septum transversum; *va*, *vv*, vitelline artery and vein; *yd*, yolk-duct; *ys*, yolk-stalk. Other letters as in Figs. 616 and 619.

the sides, where it meets oblique lateral somatic ridges running downwards along the body-wall from the mesocardia lateralia to meet the ventral mesentery below, Figs. 618-20. Thus the narrow passages between the body-wall and the liver are closed and a complete septum transversum (of His) is formed, shutting off the pericardial cavity ventral to the ductus Cuvieri. Later on the liver is to a great extent separated off from the septum transversum, remaining attached to it by coronary ligaments connected with the hepato-enteric mesentery above and the falciform ligament below. The septum transversum is then left as a peritoneo-pericardial membrane.
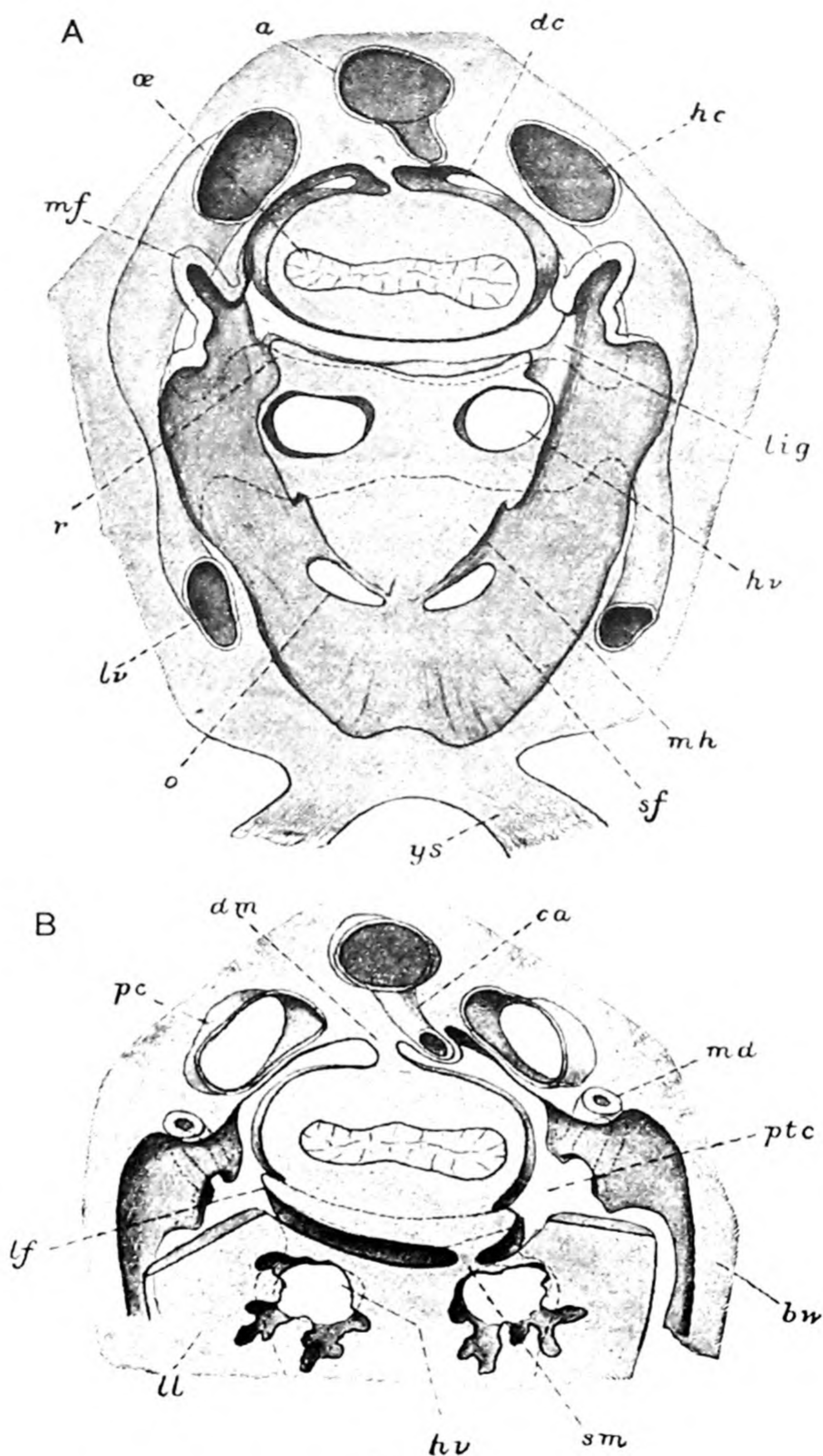
FIG. 619.

Posterior views of reconstructed thick transverse sections of an embryo *Scyllium canicula*, Stage O, about 28 mm. long, showing obliteration of dorsal coelom and formation of septum transversum. Posterior face of the section in Fig. A passes just in front of liver, and dotted line in Fig. B fits on to it ; top corners of liver cut away. *bw*, Body-wall ; *dc*, dorsal coelom ; *dm*, dorsal mesentery ; *hc*, and *pc*, posterior cardinal ; *hv*, hepatic vein ; *lf*, left mesenteric fold ; *lig*, suspensory ligament of liver ; *ll*, left lobe of liver ; *lv*, lateral vein ; *md*, Müllerian duct ; *mf*, Müllerian funnel ; *mh*, mesohepaticum anterius or falciform ligament ; *o*, opening in incomplete septum transversum ; *r*, ridge of mesenterial fold ; *sf*, somatic fold of transverse septum ; *sm*, lesser ventral or hepato-enteric mesentery.

The dorsal pericardio-peritoneal passages are later obliterated (incompletely in Cyclostomes and Selachians) by the approximation and final fusion of the splanchnic wall of the oesophagus with the somatic wall and mesocardia lateralia.

Although the septum transversum develops in the Cyclostomes much as in other Vertebrates (Goette, 964), their pericardium differs in some
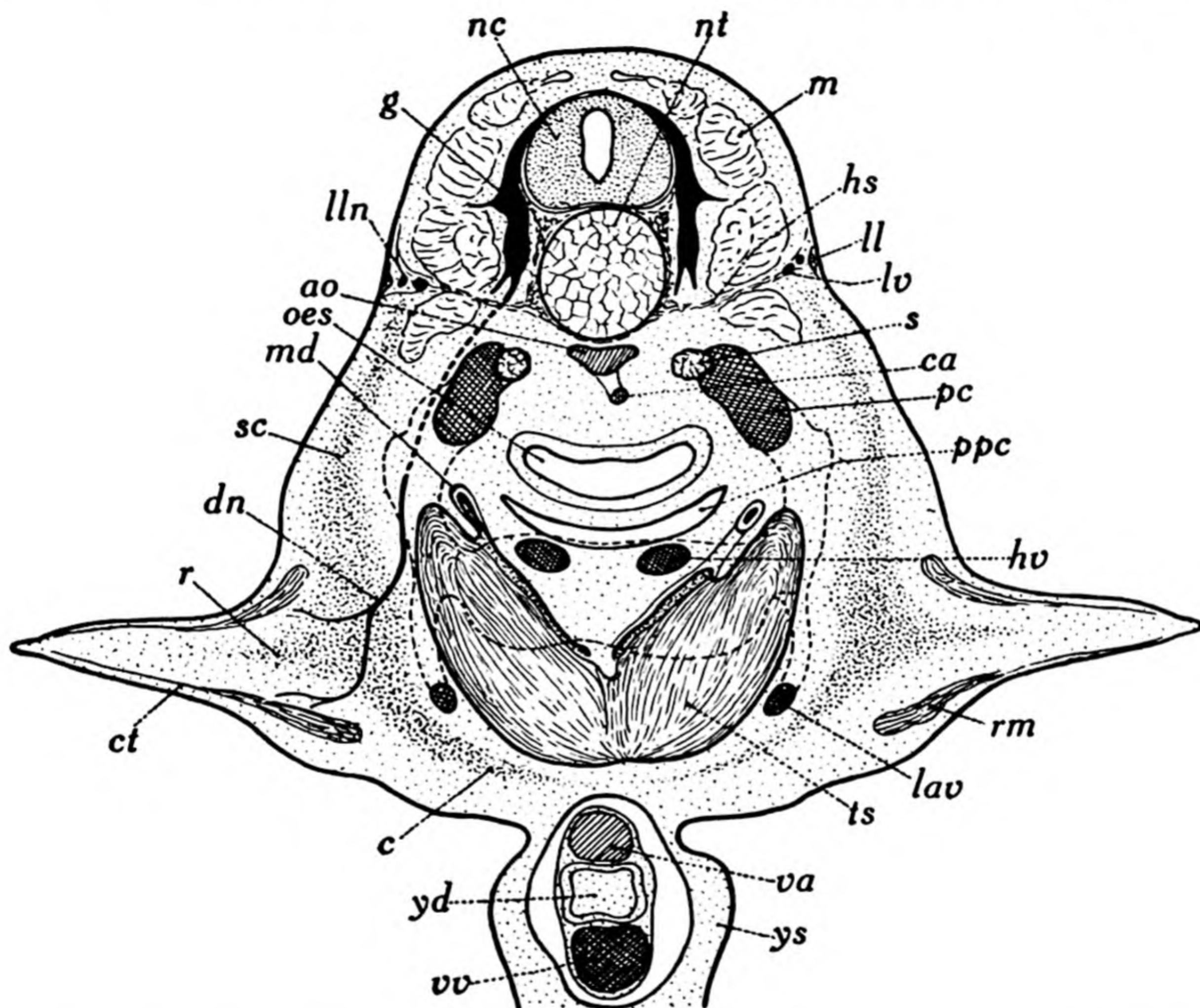
FIG. 620.

Scyllium canicula, embryo, 33 mm. long, cut transversely just in front of liver and seen from behind. *ao*, Dorsal aorta; *c*, coracoid region of procartilaginous pectoral girdle; *ca*, coeliac artery; *ct*, ceratotrich; *dn*, diazonal nerve; *g*, spinal ganglion; *hs*, horizontal septum; *hv*, hepatic vein; *lav*, lateral vein; *ll*, lateral line; *lln*, lateral-line nerve; *lv*, lateral-line vein; *nc*, nerve-cord; *nt*, notochord; *m*, myomere; *md*, Müllerian duct and funnel; *oes*, oesophagus; *pc*, posterior cardinal vein; *ppc*, passage to pericardial coelom; *r*, rudiment of radial; *rm*, radial muscle; *s*, mass of sympathetic and chromaffine cells; *sc*, scapular region; *ts*, transverse septum separating pericardial from peritoneal coelom; *va*, vitelline artery; *vv*, vitelline vein; *yd*, yolk-duct; *ys*, stalk of yolk-sac. Dotted lines show union of large veins to sinus venosus in front.

important respects. In Myxinoids the dorsal region persists in the adult at the side of the oesophagus lodging the pronephros, which extends in front of the ductus Cuvieri and is therefore supplied, in part at least, by the anterior cardinal vein (p. 508); and the pericardial cavity remains on the right in open communication with the trunk peritoneal coelom by a wide aperture, the persistent dorsal passage, Fig. 679. A similar

condition obtains in the Ammocoete larva of the lamprey, Fig. 522 (and is said to persist in the adult *Petromyzon planeri* by Broman). The closed pericardial cavity of *Petromyzon* has its wall strengthened by a cartilaginous lamella forming the posterior part of the branchial basket within which the pericardium lies.

Every student of zoology doubtless knows that the pericardial cavity communicates with the more posterior peritoneal coelom in Elasmobranchs by a canal below the oesophagus, Fig. 621, which canal bifurcates and opens behind by right and left apertures above the liver (Monro, 1783). Hochstetter maintained that these pericardio-peritoneal openings are formed late in development by a secondary piercing of the completed posterior pericardial wall (968). But it has been shown
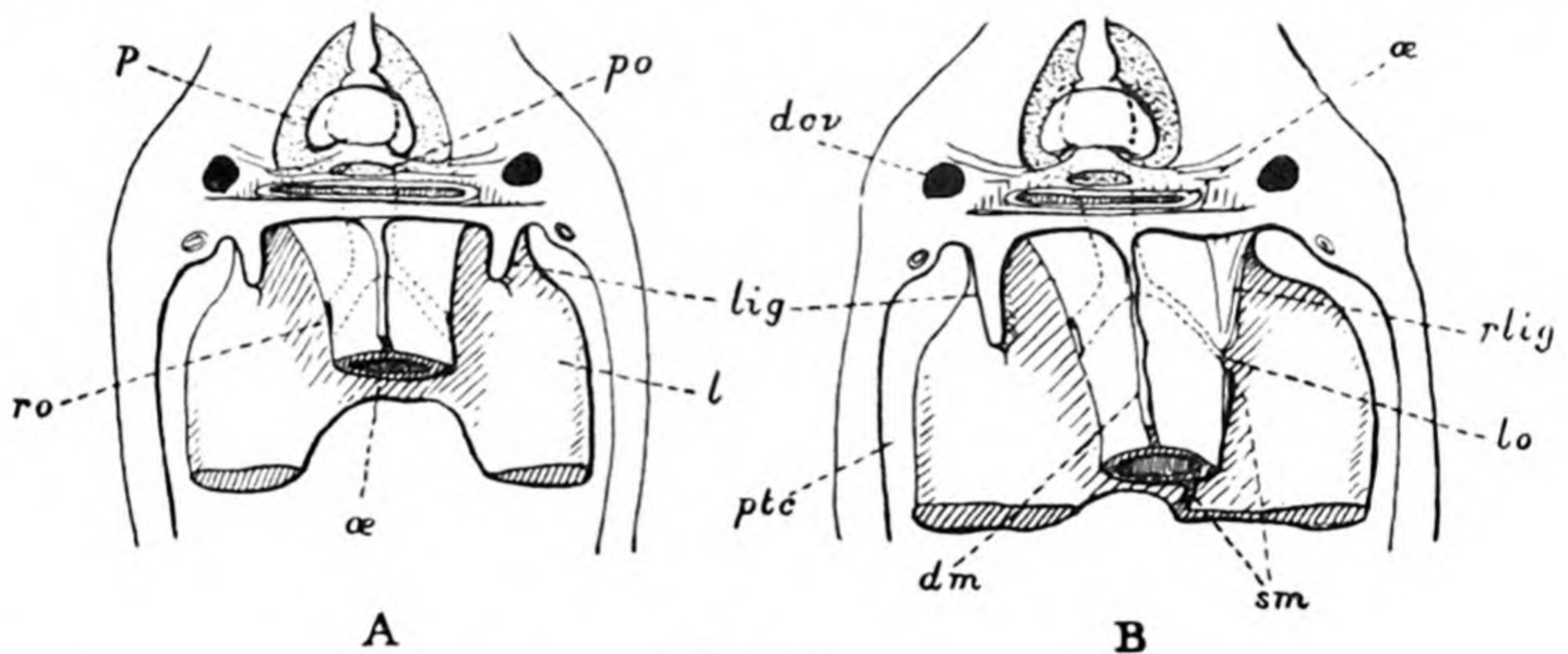
FIG. 621.

Diagrams showing relation of the suspensory ligaments of liver to mesenteries and pericardio-peritoneal canals in an adult Squalus, A, and *Scyllium*, B. Dorsal parts removed by horizontal cut; dorsal view in which canals below the oesophagus are represented by dotted lines. *dcv*, Ductus Cuvieri; *dm*, dorsal mesentery; *lig*, lateral suspensory ligament of liver, *l*; *lo*, *ro*, left and right openings of pericardio-peritoneal canals; *p*, pericardial coelom, *po*, median opening into it of pericardio-peritoneal canal; *rlig*, right lateral suspensory fold.

(Goodrich, 965) that, as Balfour suggested, they are narrow remnants of the original wider passages found in earlier stages dorsally to the mesocardia lateralia, and that in these fishes the closing off of the pericardial from the peritoneal cavities is never completed. The dorsal passages become constricted by the obliteration of the dorsal region of the pericardial coelom due to concrescence of the oesophagus with the roof and sides of the pericardial cavity, but remain as small openings, situated at first opposite and below the Müllerian funnels, and later shifting on to the ventral side of the oesophagus. A median depression of the hind wall of the pericardial coelom forms the anterior median part of the communication, and the original paired openings get carried back to their position in the adult.

Whether the pericardio-peritoneal opening in Chondrostei is likewise a remnant of the original communication does not seem to have been determined.

THE MESENTERIES AND BURSA OMENTALIS

The splanchnic coelom being of paired origin, the primitive mesentery first appears as a complete partition between the right and left coelomic cavities (Balfour, 317). It is formed of the two layers of coelomic epithelium and the intervening splanchnic mesoblast, mesenchymatous tissue surrounding the gut in the middle, the longitudinal dorsal blood-vessel or aorta above, and the longitudinal ventral vessel below, Figs. 1 and 5. Suspending the alimentary canal, the mesentery also affords access to it for blood-vessels, nerves, and lymph-channels, yet it never remains quite complete in the adult, being pierced more or less extensively by secondary perforations allowing communication from side to side. The primitive mesentery may be distinguished into a dorsal region above the gut and a ventral region below it. The dorsal mesentery remains complete in Mammals and Reptiles, but may be pierced in Birds and Amphibians, and is generally very much reduced in Selachians and Actinopterygians. With rare exceptions, such as the Anguilliformes, Dipnoi, and *Lepidosteus*, the ventral mesentery is so extensively perforated that it disappears almost entirely below the mid- and hind-gut, thus facilitating the coiling of the intestine and allowing free play for its peristaltic movements. The dorsal mesentery is often again subdivided for descriptive purposes in higher forms into the mesogastrium or great omentum, mesoduodenum, mesentery proper, mesocolon, and mesorectum, according as these various regions support the stomach, duodenum, small intestine, colon, and rectum. That portion of the ventral mesentery, lying in front of the septum transversum (see p. 536) and supporting the ventral blood-vessel which here becomes transformed into the heart, is known as the meso-cardium. It is a very transitory membrane, and soon both the dorsal mesocardium and the ventral disappear above and below the heart, Figs. 551-2.

Behind the septum transversum the ventral mesentery usually persists as the omentum minus or hepato-enteric ligament, between the gut and the liver ; and below the liver as the falciform or median ventral hepatic ligament, extending as far as the umbilicus. A small portion of the ventral mesentery may also remain below the rectum supporting the allantoic bladder. The digestive glands, being diverticula of the fore-gut immediately behind the septum transversum, grow out into the mesentery. A longitudinal ventral hepatic groove appears in the embryo and becomes subdivided into an upper anterior hepatic and a lower posterior cystic diverticulum, Figs. 618, 622, 652. The former, branching in the septum transversum and ventral mesentery, soon gives rise to a bulky
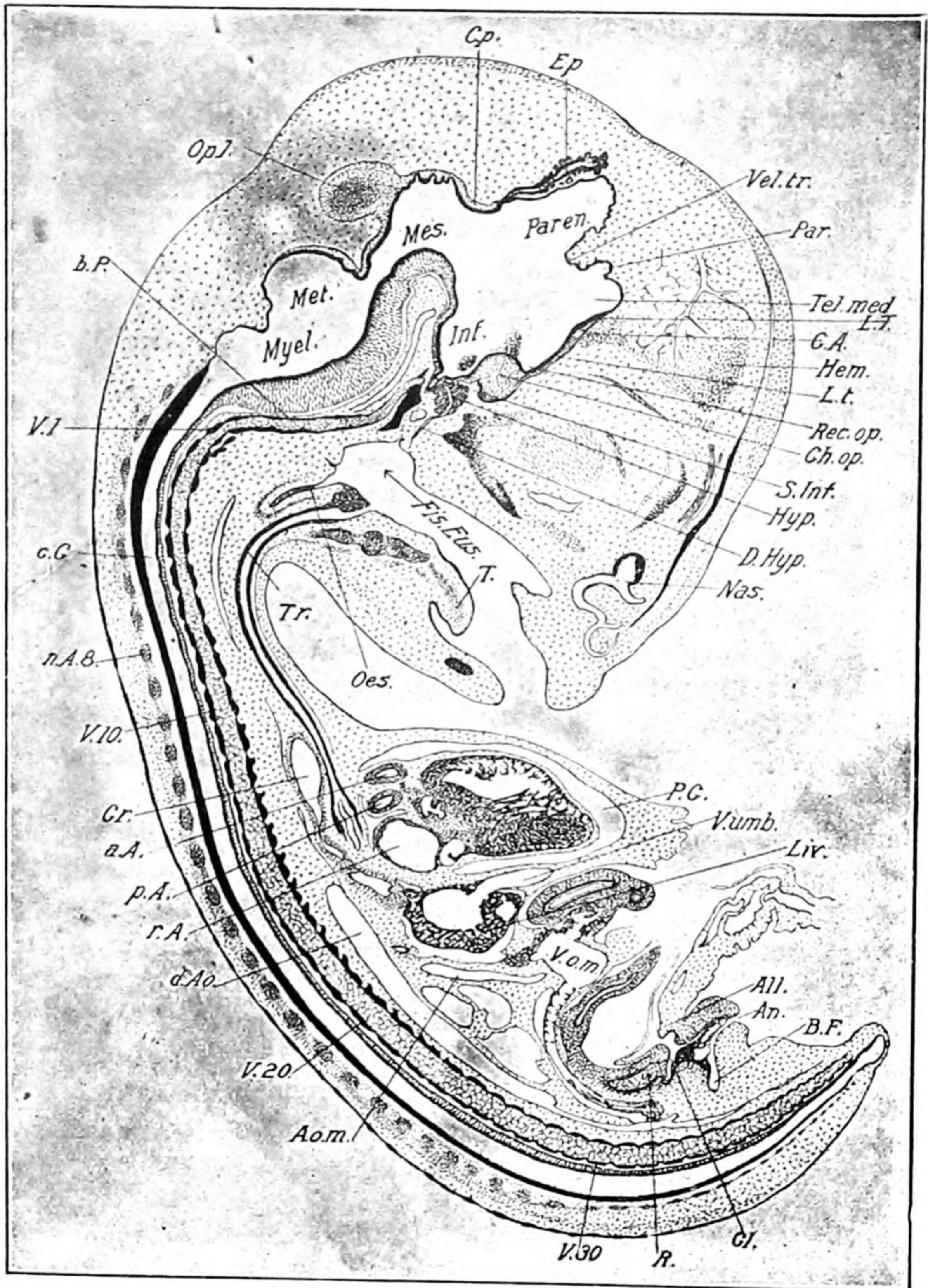
FIG. 622.

Median sagittal section of chick embryo of eight days (from F. R. Lillie, *Develt. Chick*, 1919). *a.A*, Aortic arch; *All*, allantois; *An*, anus; *A.o.m*, omphalomesenteric artery; *B.F*, bursa Fabricii; *b.P*, basilar plate; *C.A*, anterior commissure; *c.C*, central canal, *Ch.op*, optic chiasma; *C.p*, posterior commissure; *Cl*, cloaca; *Cr*, crop; *d.Ao*, dorsal aorta; *D.Hyp*, duct of hypophysis; *Ep*, epiphysis; *Fis.Eus*, fissura Eustachii; *Hem*, surface of hemisphere barely touched by section; *Hyp*, hypophysis; *L.t*, lamina terminalis; *n.A.8*, neural arch of eighth vertebra; *Nas*, nasal cavity; *Oes*, oesophagus; *p.A*, pulmonary arch; *par*, paraphysis; *P.C*, pericardial cavity; *Rec.op*, recessus opticus; *R*, rectum; *S.Inf*, saccus infundibuli; *T*, tongue; *Tel.Med*, Telencephalon medium; *Tr*, trachea; *V.1, 10, 20, 30*, first, tenth, twentieth, and thirtieth vertebral centra; *r.A*, right auricle; *Vel.tr*, velum transversum; *V.o.m*, omphalomesenteric vein; *V.umb*, umbilical vein.

liver bulging backwards into the trunk coelom. While the posterior diverticulum yields the gall-bladder, the base of the hepatic outgrowth becomes narrowed and lengthened to form the bile-duct or ductus chole-dochus, running along the ventral free edge of the lesser omentum to open into the duodenum. Two paired outgrowths from the base of the primitive hepatic diverticulum and one dorsal outgrowth from the fore-gut above them give rise to the pancreas.

The ventral pancreas, whose duct (ductus Wirsungnianus) opens at or near the base of the bile-duct, grows upwards next the stomach, and usually fuses with the dorsal pancreas ; the bulk of the ventral pancreas is derived almost exclusively from the right rudiment. The dorsal pancreas extending in the dorsal mesentery may retain its own duct (ductus Santorini).[1]

The endodermal (hypoblastic) gut of Vertebrates can be divided into fore-, mid-, and hind-gut ; the mid-gut being that portion in the ventral wall of which is stored the bulk of the yolk in the embryo. It is here that the yolk-stalk or vitelline duct is formed by the constriction of the embryo from the yolk-sac in those forms where the yolk is very abundant, and it is below this region of the gut that the ventral mesentery is invariably interrupted. From the fore-gut arise the pharynx with its gill-pouches and lungs, the oesophagus, and, immediately behind the septum trans-versum, the stomach ; lastly, the hepatic and pancreatic diverticula grow out from it just in front of the anterior portal or front end of the mid-gut. From this region backwards extends the mid-gut as far as the caecum ; it is a region variously differentiated in the different classes, and comprising the main part of the intestine. The hind-gut gives rise to the caecum, colon, and rectum, with the allantoic bladder in the higher forms.

Having thus outlined the main morphological relation of these parts, we may proceed to describe those developments which lead up to·the formation of various recesses, and especially of the lesser peritoneal cavity or bursa omentalis opening into the main peritoneal cavity by the foramen of Winslow in the Mammalia.

All the Gnathostomata have a markedly asymmetrical fore-gut, due to the development of a large well-differentiated stomach from the region lying just behind the septum transversum and in front of the hepatic

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[1] No ventral pancreas has been found in Cyclostomes and Selachians. The suggestion made by Goette and Laguesse that some of the hepatic diverticula may represent it seems not to be justified (Brachet, 993). It is possible that the function of the ventral pancreas differs from that of the dorsal.

diverticulum. Since the anterior end of the duodenum remains, so to speak, firmly held in place by the lesser omentum and contained bile-duct, the gut is bent to the left to accommodate the growing stomach carrying the mesenteries with it.   A depression is thus formed on the right side of the mesentery and extending over the dorsal side of the stomach and backwards between the stomach, spleen, and pancreas; it is the first beginning of a bursa omentalis, or rather that region of it distinguished later as the bursa omenti majoris.

This is the condition of the bursa omentalis in the Selachian embryo (Phisalix, 1885; Broman, 959), where it is a shallow depression widely
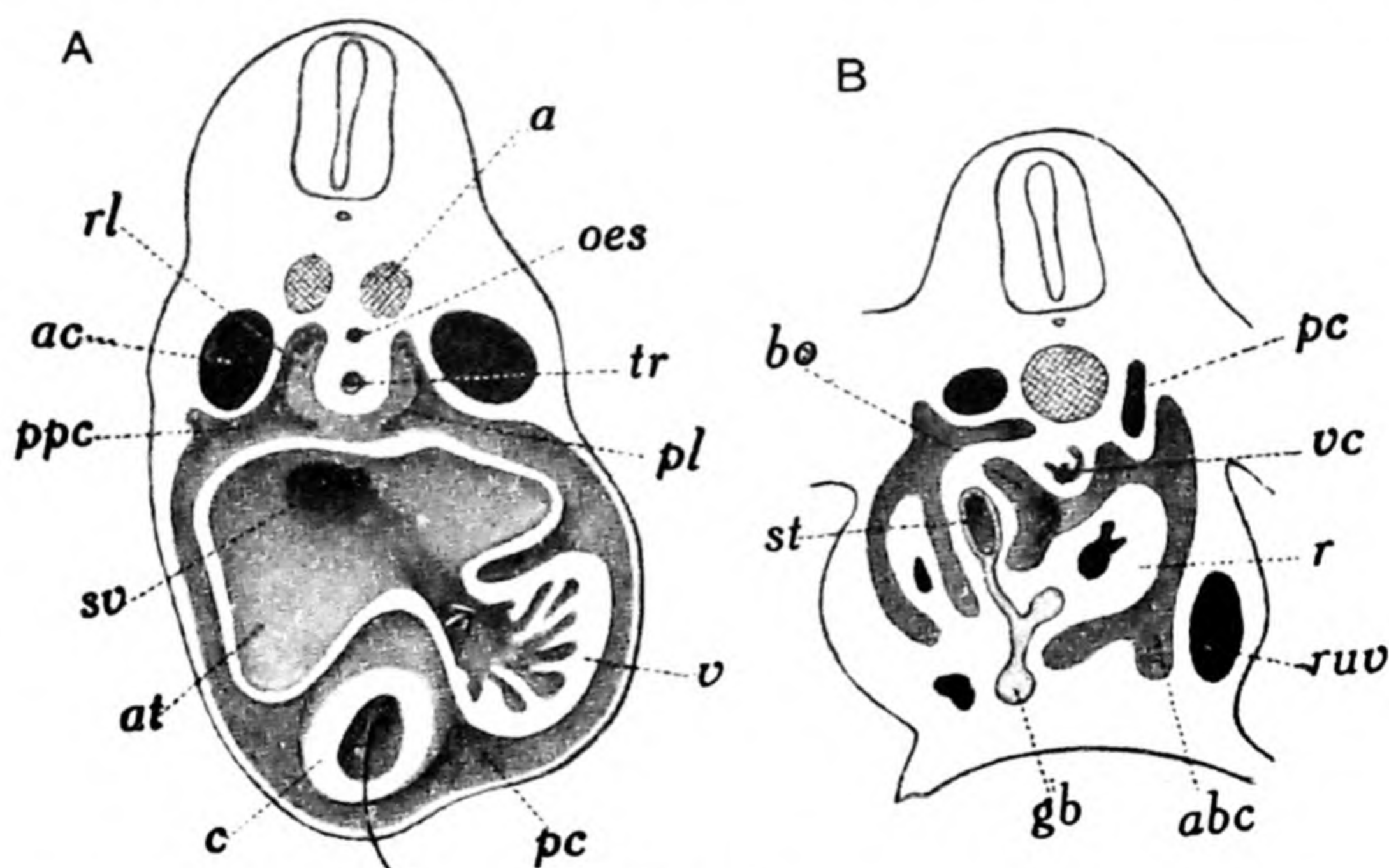
FIG. 623.

Mus musculus, embryo cut transversely and reconstructed. A, Through pericardial region, anterior view; B, through stomach, posterior view. *a*, Aorta; *abc*, abdominal (peritoneal) coelom; *ac*, right anterior cardinal; *at*, atrium; *bo*, bursa omentalis; *c*, bulbus cordis; *gb*, gall-bladder; *oes*, oesophagus; *pc*, right posterior cardinal; *pl*, pleural coelom; *ppc*, pleuro-peritoneal passage; *r*, right lobe of liver; *rl*, right lung bud; *ruv*, right umbilical vein; *st*, stomach; *sv*, opening to sinus venosus; *tr*, trachea; *v*, ventricle; *vc*, vena cava inferior.

open to the general trunk coelom on the right, and marked off above by an overhanging ridge of the dorsal mesentery, the plica mesogastrica, but leading back to a deep blind pocket between the stomach and pancreas, the recessus pancreatico-entericus. This latter recess opens behind the coeliac artery, which becomes freed from the mesentery at a very early stage. In later development the mesentery becomes so defective that scarcely any trace of the bursa remains in the adult; and the same may be said of most of the Pisces.

Already in the Dipnoi, however, begin to appear the important changes and complications characteristic of the Tetrapoda, and correlated for the most part with the development of the lungs and the vena cava. In

these higher Vertebrates, the stomach becomes more differentiated and more bent away from the middle line, and the bursa omentalis correspondingly enlarged and deepened, Figs. 628, 650. Pushing its way between the mesenteries and viscera, and tending to wrap round the alimentary canal, it forms special recesses which all communicate with the general trunk coelom on the right by an opening, the hiatus communis recessum (primitive foramen of Winslow), behind the liver. Dorsally the recessus pancreaticus-entericus extends back into a blind pocket spreading over the right surface of the stomach; ventrally a recessus hepato-entericus, bounded below by the lesser omentum, extends forwards above the liver where it passes into the right pneumato-enteric recess, the origin of which will be described below. The hiatus communis recessum or primitive foramen of Winslow is at first large and without definite posterior margin; but it gradually becomes constricted by surrounding structures. It is bounded in front by the liver, above by the plica mesogastrica, and below by the edge of the lesser omentum holding the portal vein, hepatic artery, and bile-duct. The plica mesogastrica contains the vena cava inferior (thus forming the dorsal fold called Höhlenvenengekröse by Hochstetter, and Vena-cava-falte by Ravn), and, as the right dorso-lateral lobe of the liver grows backwards along the vein into the fold, the opening becomes restricted from in front. Further, in the Amniota, the coeliac artery and its branch the hepatic artery draw out a fold from the mesentery projecting on the right and from behind, so that the plica mesogastrica now splits into an outer plica venae cavae and an inner plica arteriae coeliacae; a small cavo-coeliac recess between them becomes the atrium or vestibulum bursae omentalis, just within the foramen epiploicum Winslowi in the mammal. The coeliac fold tends to separate the bursa omenti majoris on the left from the bursa omenti minoris on the right.

THE PULMONARY FOLDS AND RECESSES

An important new feature in the anatomy of the air-breathing vertebrates is the outgrowth from the wall of the oesophagus of an accessory mesentery, lateral mesenterial or pulmonary fold (Nebengekröse, pulmo-hepatic ligament of Butler, mésolatéral of Brachet), to support the lung. When the mesoblastic pulmonary thickening grows outwards and backwards from the pharynx a pocket is formed behind it into whose outer wall pushes the hypoblastic lung-bud. This outer wall becomes later developed into a membrane, subdivided by the lung into a dorsal 'pulmonary ligament' attached to the median mesentery above, and a ventral 'pulmonary ligament' attached to the edge of the lateral lobe

of the liver below, Figs. 624, 630. We shall call these membranes,
ligaments or accessory mesenteries, simply the right and left pulmonary folds. In front this pulmonary fold is attached to the oesophagus, the root of the lung, and the septum transversum above the sinus venosus; it passes, therefore, on the inner side of the original pericardiaco-pleuro-peritoneal communications, while the nephric fold passes to the outer side of these openings (see p. 631). Thus a deep recess may be cut off from the general peritoneal cavity on either side of the median mesentery between it and the pulmonary folds, or in other words between the oesophagus, lung, and liver, Figs. 628-9. These pulmonary or pneumato-enteric recesses (pulmo-hepatic recesses of Butler, 962-3) are blind in front, but open behind the free edge of the
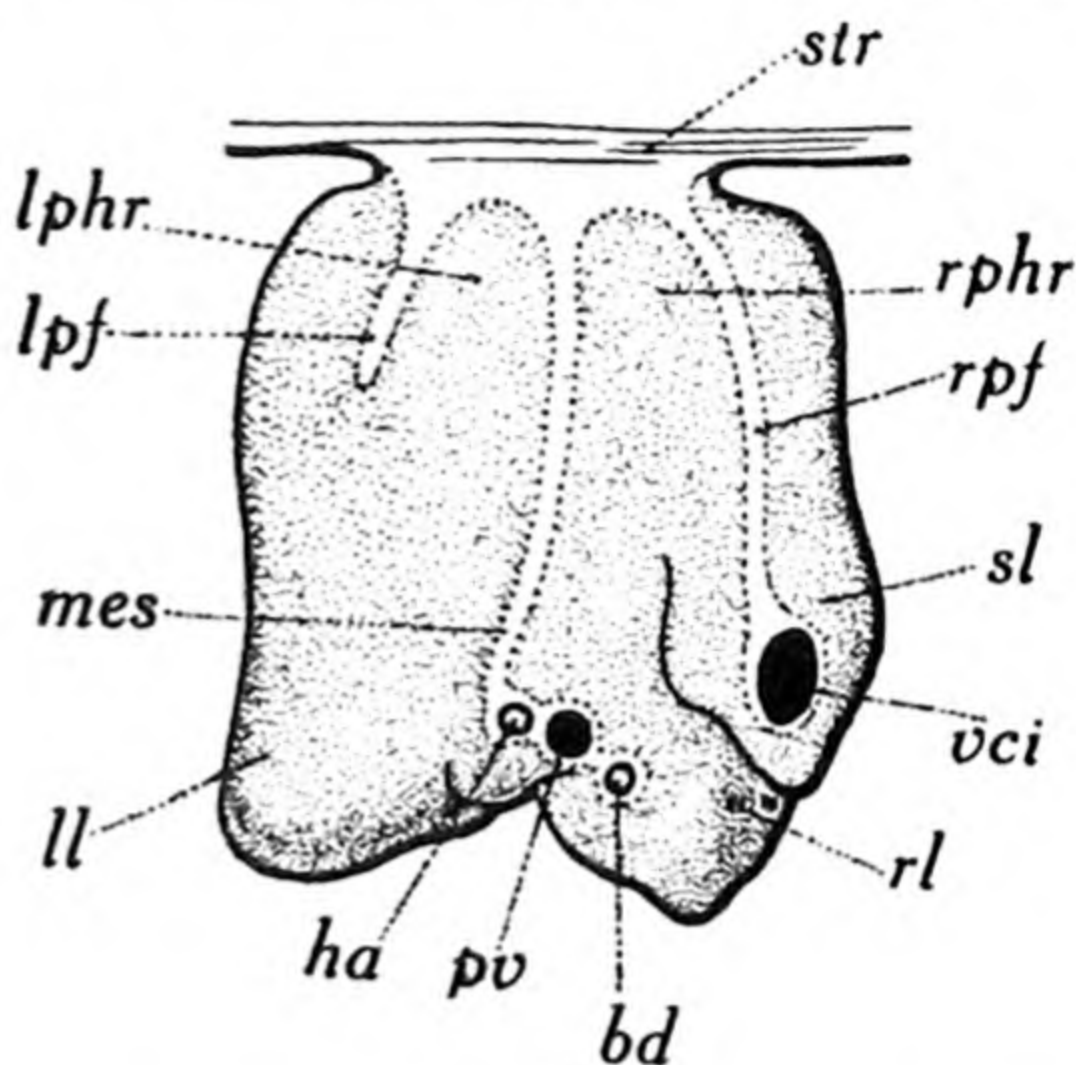
FIG. 624.

Diagram of dorsal surface of liver of a Tetrapod (modified from Broman); white areas bounded by dotted line indicate attachments of median mesentery, *mes*, left pulmonary fold, *lpf*, and right pulmonary fold, *rpf*. *bd*, Bile duct; *ha*, hepatic artery; *ll*, left lobe of liver; *lphr*, left pulmohepatic recess; *pv*, portal vein; *rl*, right lobe; *rphr*, right pulmohepatic recess; *sl*, dorsal lobe; *str*, hind surface of septum transversum; *vci*, vena cava inferior.
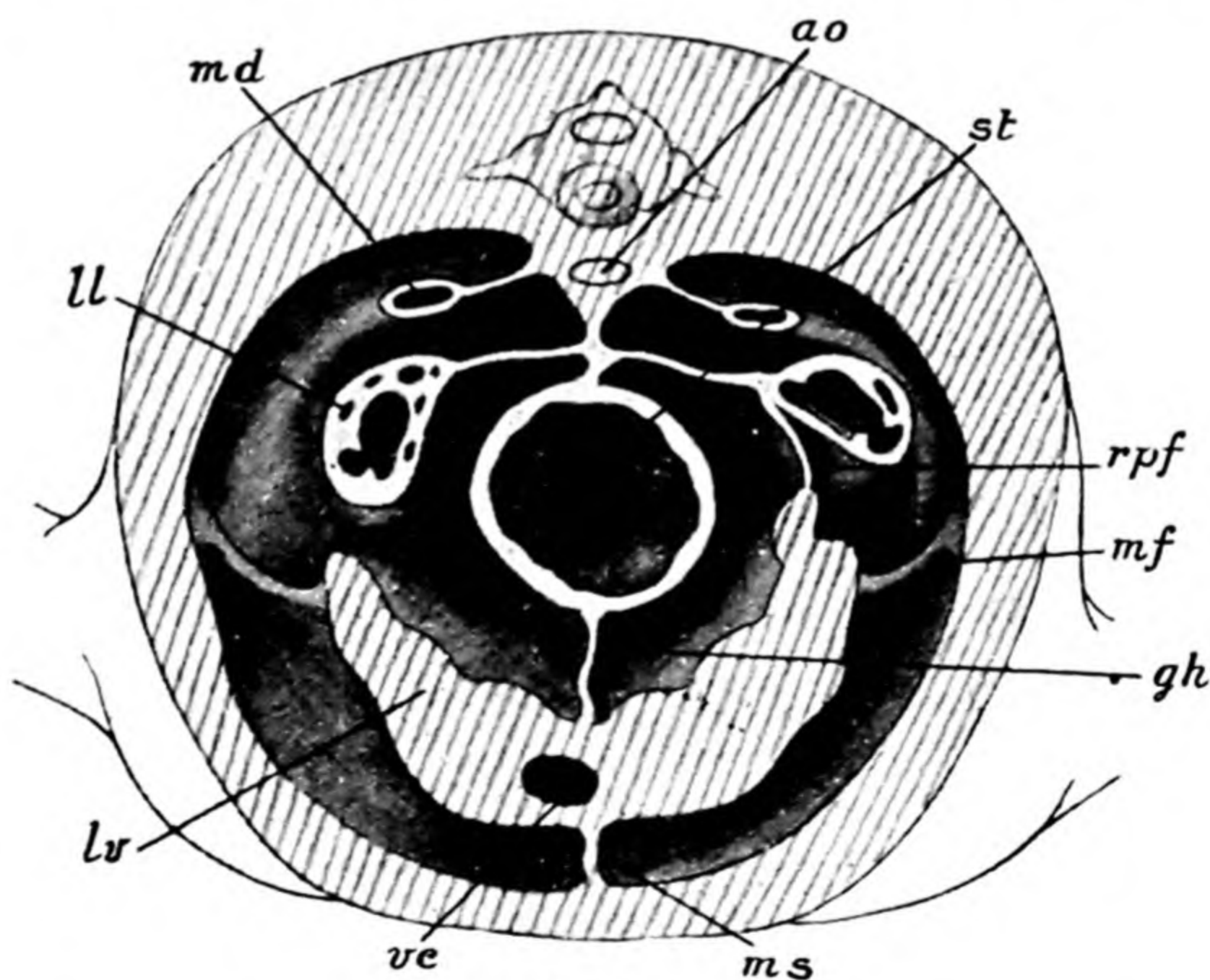
FIG. 625.

Salamandra maculosa, ♀; cut transversely through anterior trunk region and viewed from behind. *ao*, Dorsal aorta; *gh*, gastro-hepatic region of mesentery; *ll*, left lung; *lv*, liver; *md*, Müllerian duct suspended by nephric fold; *mf*, Müllerian (oviducal) funnel; *ms*, subhepatic mesentery; *rpf*, right pulmonary fold closing right pulmonary recess; *st*, stomach; *vc*, vena cava inferior.

pulmonary folds. Generally the lungs bulge on the outer surface
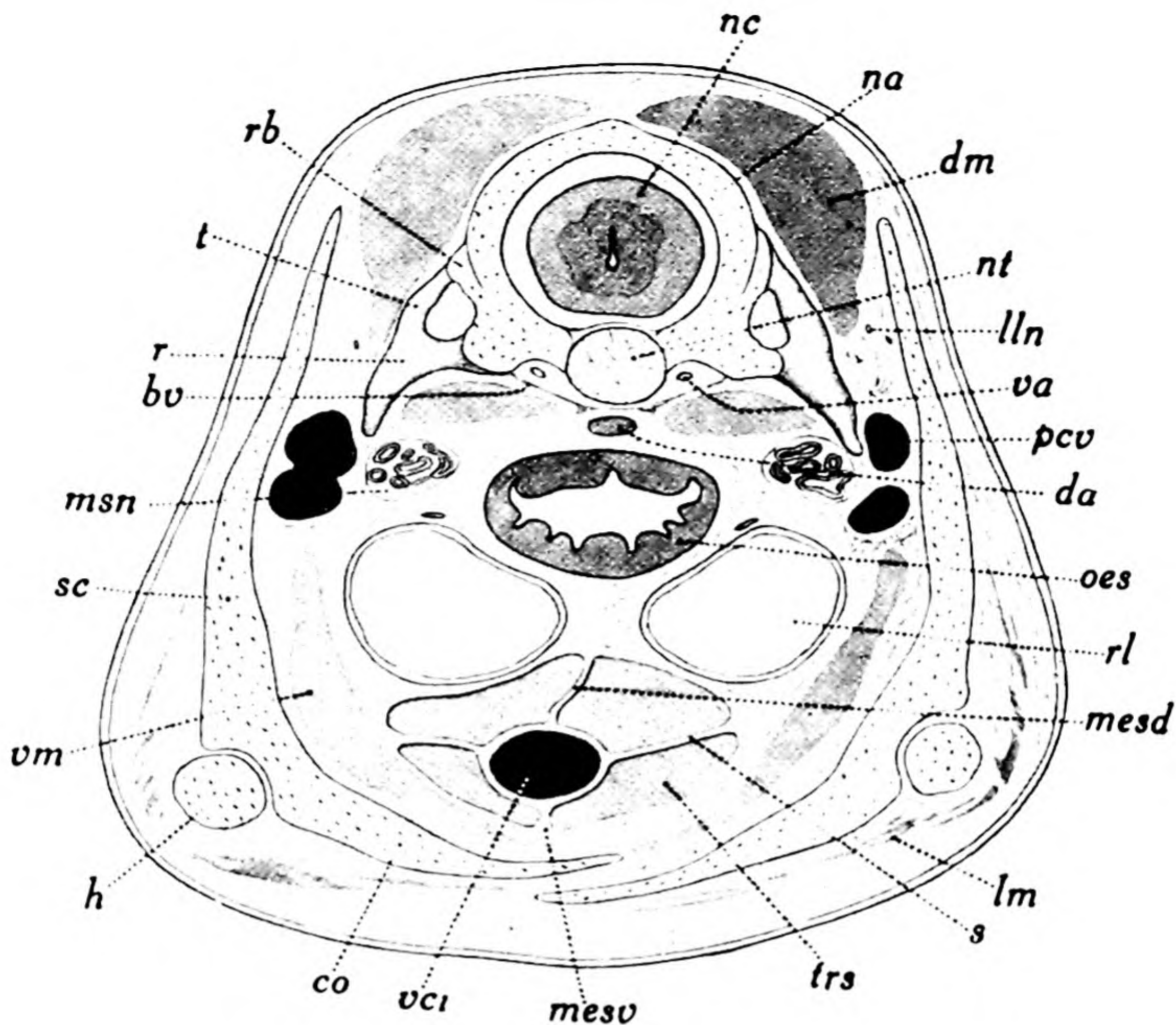
FIG. 626.

Salamandra, larva. Reconstructed thick transverse section, posterior view. *bv*, Ligament from rib to vestigial basiventral ; *co*, coracoid region ; *da*, dorsal aorta ; *dm*, dorsal muscles ; *h*, humerus ; *lln*, lateral-line nerve ; *lm*, limb muscles ; *mesd*, dorsal mesentery ; *mesv*, ventral mesentery ; *msn*, mesonephros ; *na*, neural arch ; *nc*, nerve cord ; *nt*, notochord ; *oes*, oesophagus ; *pcv*, posterior cardinal vein ; *r*, rib ; *rb*, rib-bearing cartilage ; *s*, lateral septum (part of nephric fold) ; *sc*, scapular region ; *t*, tuberculum ; *trs*, transverse septum closing pericardial cavity ; *va*, vertebral artery ; *vci*, vena cava inferior ; *vm*, ventral muscles.
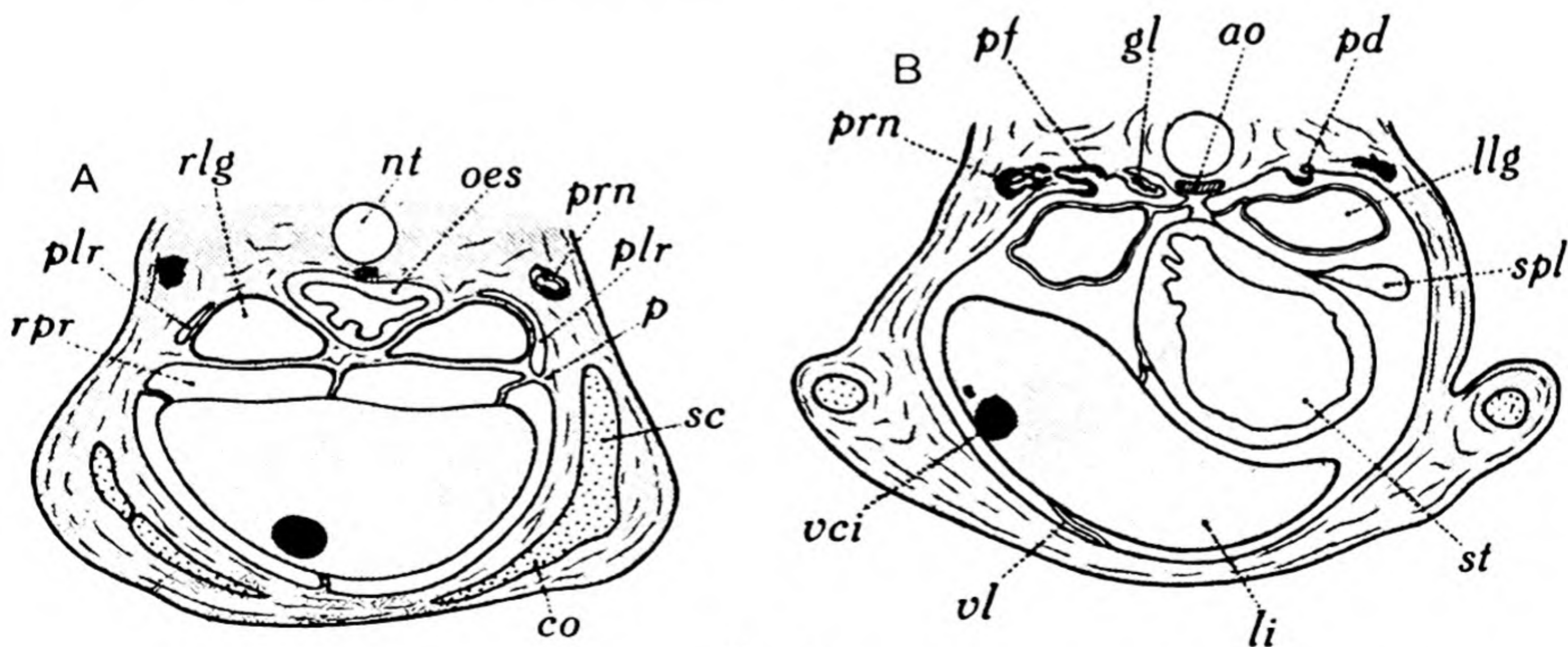
FIG. 627.

Amblystoma tigrinum, transverse sections of larva 28 mm. long. A, Through pectoral girdle ; B, farther back. *ao*, Dorsal aorta ; *co*, coracoid plate ; *gl*, glomus ; *li*, liver ; *llg*, left lung ; *nt*, notochord ; *oes*, oesophagus ; *p*, point of fusion between pulmonary fold and coelomic wall ; *pd*, pronephric duct ; *pf*, pronephric nephrocoelostome ; *rlg*, right lung ; *rpr*, right pulmonary recess ; *sc*, scapular region ; *spl*, spleen ; *st*, stomach ; *vci*, vena cava inferior ; *vl*, ventral mesentery.

of the pulmonary folds into the pleural region of the coelom, and their posterior tips may grow out freely. As a rule, the left pulmonary fold (ligamentum-hepato-pulmonale of Mathes, 973) is much less developed than the right (ligamentum-hepato-cavo-pulmonale of Mathes, 973); and although its dorsal region may stretch far back, its ventral pulmonary ligament bounding the wide aperture into the general peritoneal cavity is usually much shorter, so that the left recess becomes much reduced. Indeed in all the Mammalia the left pulmonary fold and recess are quite
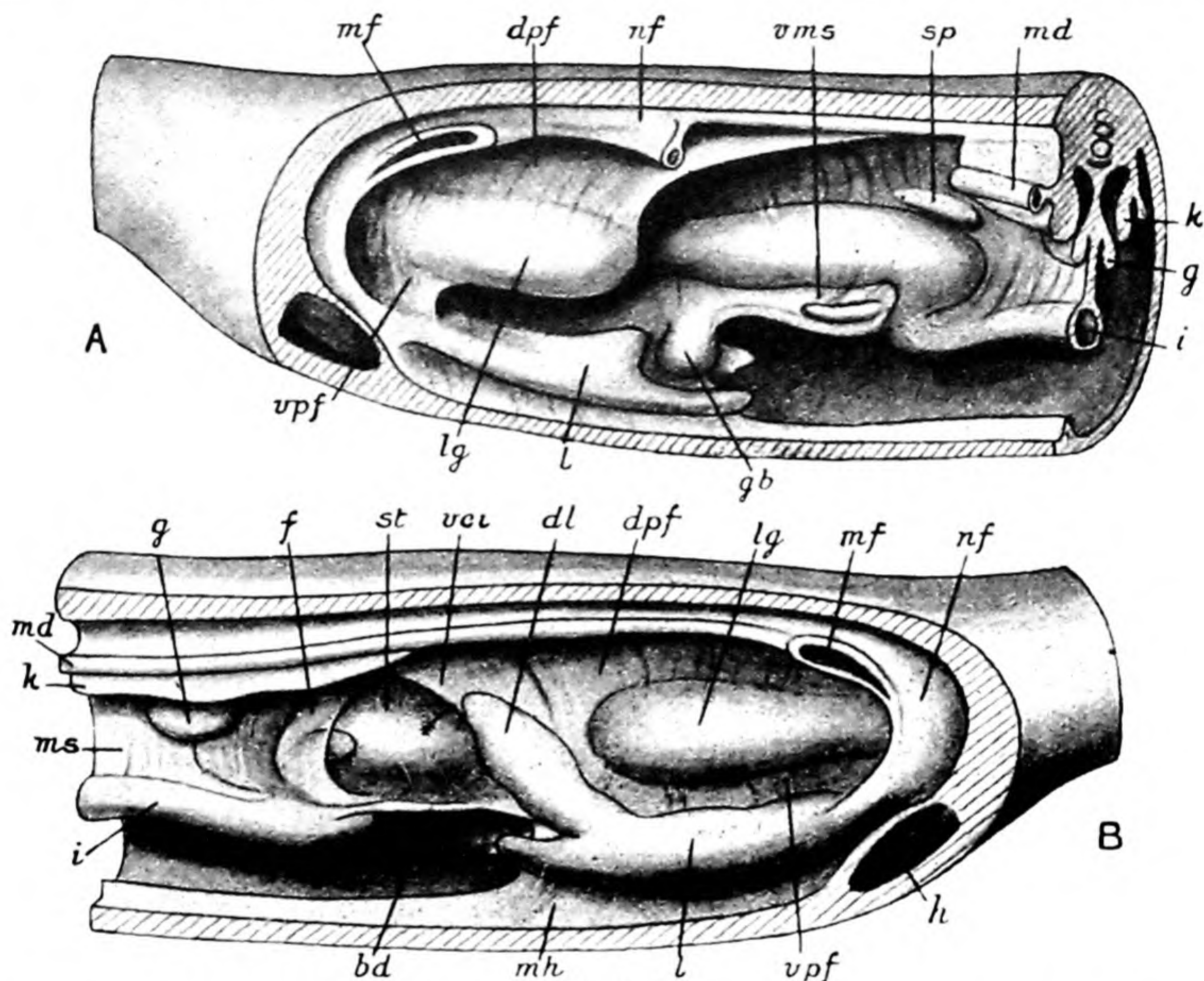
FIG. 628.

Diagram of anterior trunk region of a Tetrapod (Lizard), cut longitudinally so as to expose inner view of left side in A, and right side in B. *bd*, Bile duct ; *dl*, dorsal lobe of liver in dorsal pulmonary fold, *dpf* ; *f*, fold ; *g*, gonad ; *gb*, gall-bladder ; *i*, intestine ; *k*, mesonephros ; *l*, liver ; *lg*, lung ; *md*, Müllerian duct (part of it cut away in A) ; *mf*, its funnel ; *mh*, subhepatic mesentery ; *nf*, nephric fold ; *sp*, spleen ; *st*, stomach ; *vci*, vena cava inferior ; *vms*, ventral mesentery ; *vpf*, ventral pulmonary fold. An arrow passes into pulmonary recess.

vestigial even in the embryo, and unrecognisable in the adult. On the other hand, the right pulmonary fold is usually fully developed. Its dorsal fold extends backwards as the plica mesogastrica, and becomes converted into the plica venae cavae, being invaded by the vena cava and the dorso-lateral lobe of the liver growing up into its posterior margin. Therefore the right pneumato-enteric recess is continuous above the liver with the recessus hepato-entericus, and opens into the general peritoneal cavity, not independently like the left recess, but in common with the

other mesenterial recesses by the primary foramen of Winslow (hiatus communis). The bursa omentalis extends, then, not only into the bursa omenti majoris and bursa omenti minoris, but also forwards into the recessus pneumato-entericus. That dorsal region of the liver which is included between the mesentery and the pulmonary fold, and forms the floor of the bursa, develops into the Spigelian lobe ; a corresponding lobe
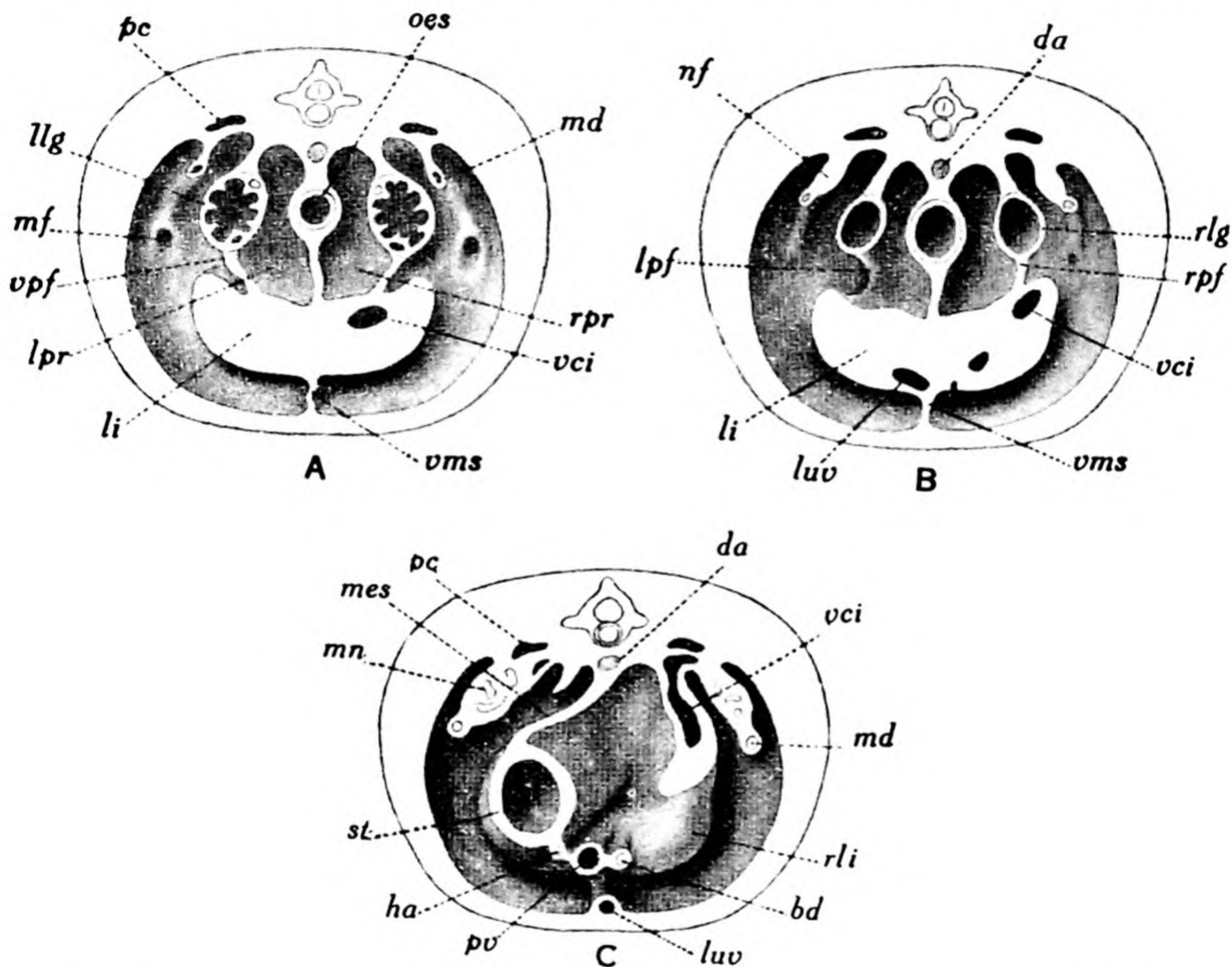
FIG. 629.

Diagrammatic transverse sections through a Tetrapod (Lacertilian) showing subdivision of splanch-nocoele. A, Far forward ; B, through hind end of lungs ; C, behind lungs. All seen from behind. *bd*, Bile duct ; *da*, dorsal aorta ; *ha*, hepatic artery ; *li*, liver ; *llg*, left lung ; *lpf*, left pulmonary fold ; *lpr*, left pulmonary recess ; *luv*, left umbilical vein ; *md*, Müllerian duct, and *mf*, its funnel ; *mes*, dorsal mesentery ; *mn*, mesonephros ; *nf*, nephric fold ; *oes*, oesophagus ; *pc*, posterior cardinal ; *pv*, portal vein ; *rlg*, right lung ; *rli*, right lobe of liver ; *rpf*, right pulmonary fold ; *rpr*, right pulmonary recess ; *st*, stomach ; *vci*, vena cava inferior ; *vms*, ventral mesentery ; *vpf*, ventral part of pulmonary fold.

may be delimited on the left side in those forms where the left pulmonary fold is well developed.

Certain modifications of the mesenteries and recesses in the various classes of the Tetrapoda may now be noticed (Broman, 959, 960).

Amphibia.—Although normally developed in the embryo, the recesses usually become much modified in the adult, especially in the Anura. In

these amphibians the hiatus communis recessum persists ; but the re-
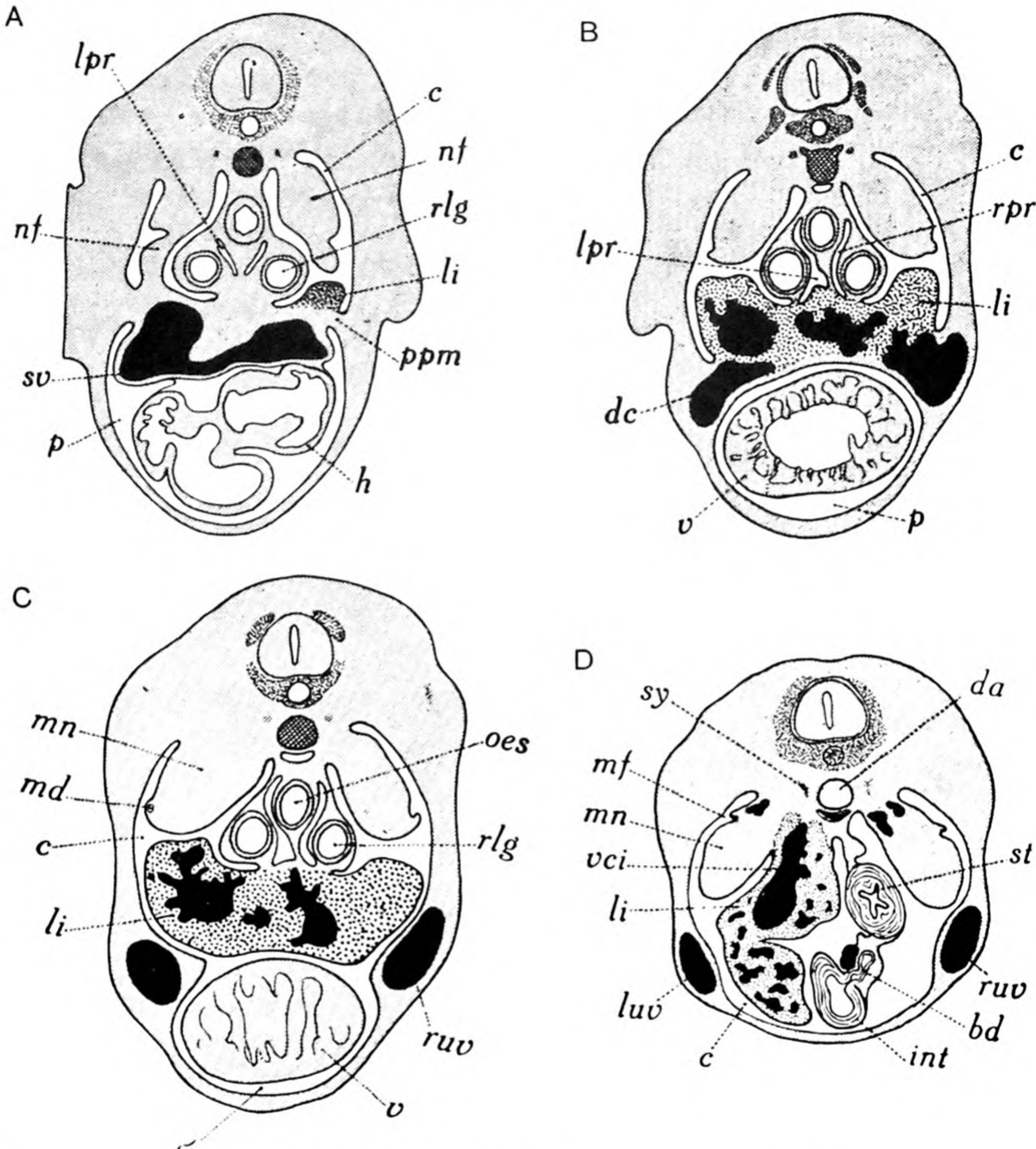
FIG. 630.

Transverse sections of embryo *Lacerta*, before closure of pericardial coelom. A, Most anterior, through septum transversum ; D, most posterior. *bd*, Bile duct ; *c*, general splanchnic coelom ; *da*, dorsal aorta ; *dc*, ductus Cuvieri ; *h*, heart ; *int*, intestine ; *li*, liver ; *lpr*, left pulmonary recess ; *luv*, left umbilical vein ; *md*, Müllerian duct ; *mf*, Müllerian funnel ; *mn*, mesonephros ; *nf*, nephric fold ; *oes*, oesophagus in mesentery between pulmonary recesses ; *p*, pericardial coelom ; *ppm*, pericardio-peritoneal membrane ; *rlg*, right lung in pulmonary fold ; *rpr*, right pulmonary recess ; *ruv*, right umbilical vein ; *st*, stomach ; *sv*, sinus venosus ; *sy*, sympathetic ; *v*, wall of ventricle ; *vci*, vena cava inferior.

cesses almost entirely disappear owing to the reduction of the pulmonary

folds and the perforation of the omentum minus. The left pneumato-enteric recess generally is very small, as the accessory mesentery is much reduced ventrally, in the Urodela, Figs. 625-7, and Gymnophiona; but the bursa omentalis is well developed, formed as usual by the combination of the right pneumato-enteric recess with the hepato-enteric and the pancreatico-enteric recesses. However, except in *Cryptobranchus* and *Menopoma*, it seems always to be completely shut off on the right by the closure of the hiatus due to the fusion of the posterior edge of the pulmonary fold with the median mesentery. Communication with the general coelom is then brought about by the perforation of the dorsal mesentery (except in *Amphiuma*).

Reptilia.—As a rule the recesses are well marked in the adult, Figs. 628-
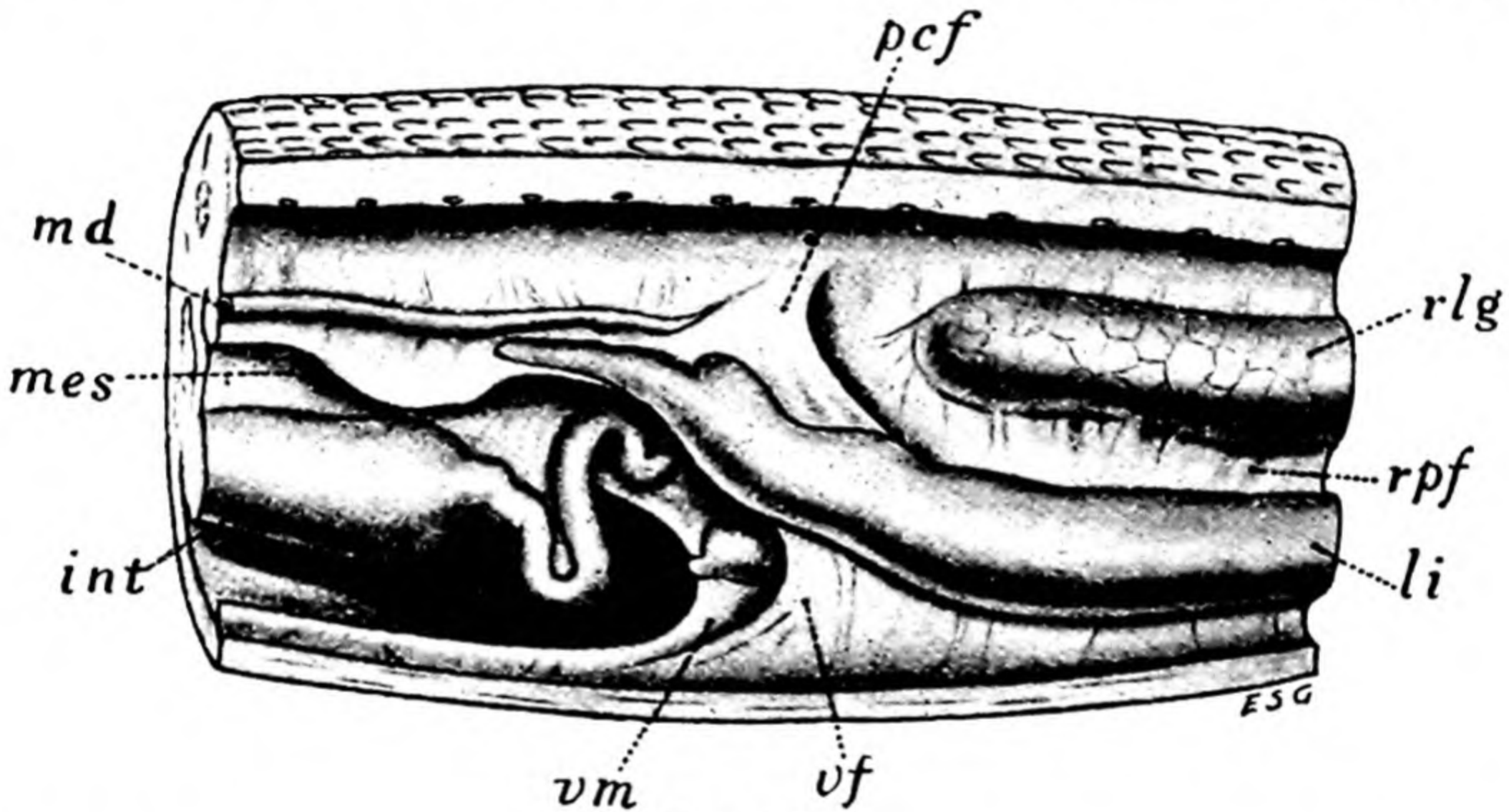
FIG. 631.

Egernia Cunninghami, ♀; right-side view of mid-trunk opened by removal of body-wall. *int*, Intestine; *li*, liver; *md*, Müllerian duct; *mes*, dorsal mesentery; *pcf*, posterior closing fold; *rlg*, hind end of right lung; *rpf*, right pulmonary fold; *vf*, ventral lateral fold; *vm*, ventral mesentery (subhepatic ligament).

631, the primitive foramen of Winslow remains large and open (except in Amphisboenids and some Chelonia, *Emys*), and the plica arteriae coeliacae is much developed, especially in Lacertilia, partially cutting off an extensive bursa omenti majoris. The lizard *Agama* has a dorsal right recessus pneumato-entericus communicating as usual with the recessus hepato-entericus, as well as a ventral right recessus pneumato-entericus opening independently to the general trunk coelom. In the Tejidae, Anguidae, *Gongylus*, and Amphisbaenidae, the right pneumato-enteric recess also opens independently (Broman).

The condition of the recesses and mesenteries in the Aves is complicated by the development of air-sacs and a post-hepatic septum, a structure already found in the Tejidae and Crocodilia, whose origin will be discussed later (p. 641), Figs. 633, 640.

Mammalia.—The left pneumato-enteric recess is here vestigial, disappearing in the adult, and often scarcely visible even in the embryo. On the right, all the recesses join to open by the clearly circumscribed foramen of Winslow ; but the anterior tip of the pneumato-enteric recess becomes nipped off by the diaphragm as a separate small closed cavity in the thorax (see p. 654).   Accompanying the rotation of the stomach to the left there is a great development of the mesogastrium, forming a large ventral sac, the great omentum, enclosing an extension of the bursa omenti majoris.   The walls of this sac usually come together in the adult so as to obliterate the cavity.

THE NEPHRIC FOLDS

Yet another peritoneal fold remains to be described which plays an important part in the subdivision of the trunk coelom in the higher Vertebrates (Bertelli, 954 ; Rabl, 1049 ; Hochstetter, 967).   In the Selachian, Figs. 619, 669, 670, a longitudinal fold runs forwards on each side along the dorsal wall of the trunk coelom from the anterior end of the mesonephros to the body-wall just behind the ductus Cuvieri and septum transversum, along which it passes to the dorsal edge of the lateral lobe of the liver.   Primitively this nephric fold (a name we prefer to that of pronephric or mesonephric fold applied to it by most authors) is derived from the nephric ridge in which develop the pronephros in front and the mesonephros farther back, Figs. 628-30.   In the female sex it remains as the mesorchium, a mesenterial fold supporting the Müllerian funnel and duct.   Now these nephric folds are constant and important features in the anatomy of Craniates, being especially well developed in the higher Gnathostomes, where they undergo many modifications, tending to separate off a pleural division of the coelom in Reptiles, and contributing to the diaphragm in Mammals.   The early stages in their development are very similar in all Gnathostomata, see Figs. 620, 629, 633, where they are seen bearing the oviducal funnel on their free edge and cutting off an anterior coelomic recess on each side.   But they are situated on the outer side of the embryonic dorsal pericardiaco-peritoneal passage, and must not be confused with the true accessory mesenteries or pulmonary folds of the air-breathing vertebrates which are situated on the inner side of these passages next to the oesophagus.[1]

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[1] The paired hepatic mesenterial folds described by Goette in the larva of *Petromyzon* are therefore nephric folds and not accessory mesenteries as he and Maurer state.

THE COELOMIC SEPTA IN AVES

We may now pass to the consideration of the various septa which subdivide the coelom in Birds, a subject which has long attracted the interest of anatomists since the days of Aristotle, yet is still but incompletely understood. The avian heart is situated far back, the pericardium resting immediately on the sternum or, as in Passeres, separated from it by a backward extension of the interclavicular air-sac; the compact lungs are pressed close up against ribs and vertebral column, the intermediate air-sacs passing down from them along the inner side of the body-wall; the large liver reaches forward, its lateral lobes extending on
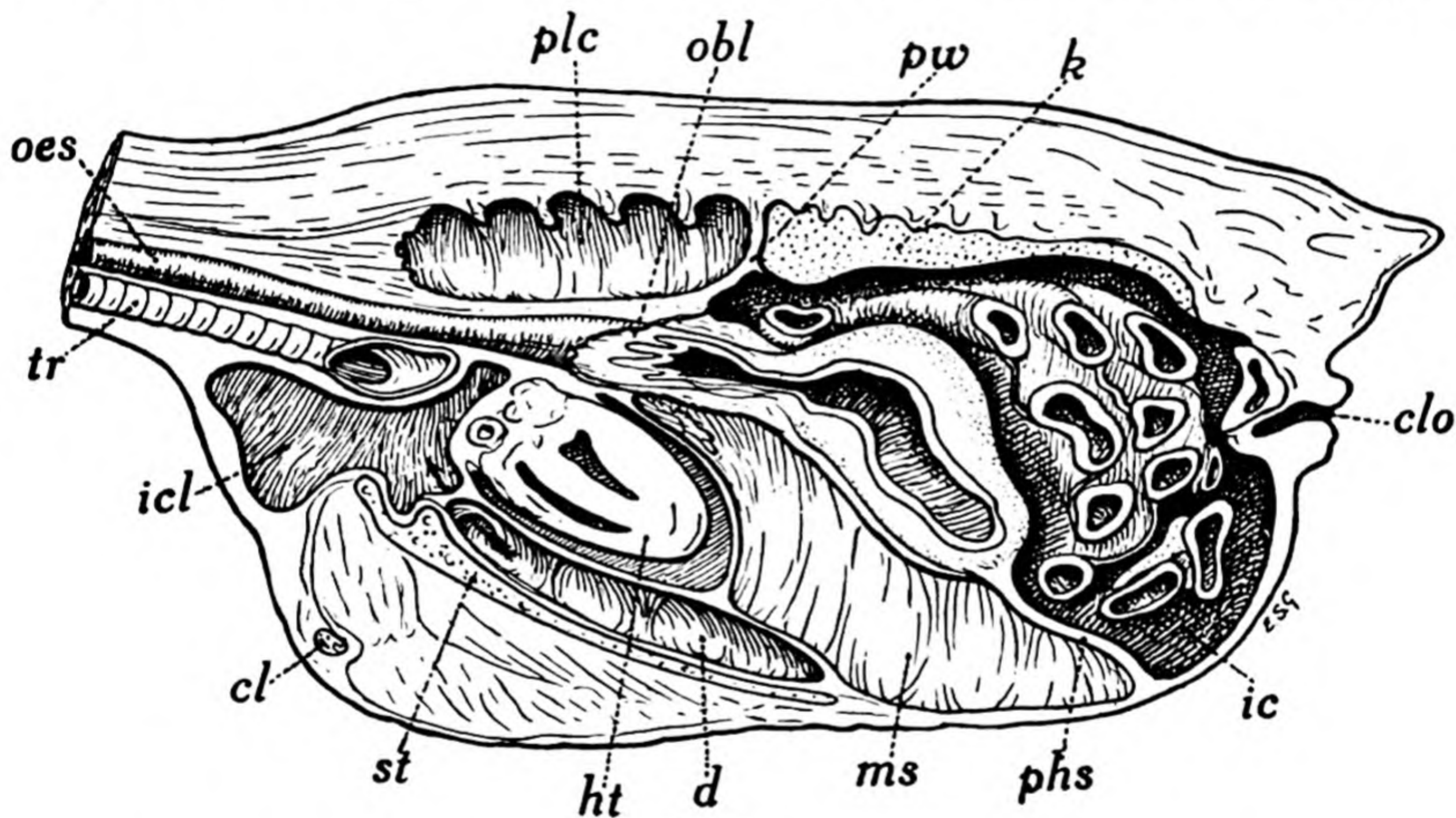
FIG. 632.

Corvus corone, inner view of right half cut longitudinally to left of middle line. cl, Clavicle; clo, cloacal aperture; d, diverticulum of interclavicular sac; ht, heart in pericardial coelom; k, kidney; ic, intestinal chamber of coelom; icl, interclavicular air-sac; ms, ventral mesentery; obl, top of oblique septum; oes, oesophagus; phs, post-hepatic septum; plc, left pleural coelom (lung removed); pw, posterior wall of pleural cavity; st, sternum; tr, trachea.

either side of the pericardium and backwards beyond it, Figs. 608-9. The disposition of the viscera is thus very different from that seen in the Mammalia, where the liver is pushed back and the pericardium flanked by the lungs. In addition to the median mesentery and the pericardial wall or pericardio-peritoneal membrane, four membranous partitions may be distinguished in birds subdividing the body-cavities—three longitudinal and one obliquely transverse. The first longitudinal membrane stretches almost horizontally across the thoracic region, really in two halves running from its attachment to the median mesentery to the body-wall below the lungs, which adhere to its dorsal surface. This

more dorsal membrane, the pulmonary aponeurosis of Huxley, 911 (diaphragme pulmonaire of Sappey, diaphragmite antérieur of Milne-Edwards, diaframmo ornitico of Bertelli), in front joins the cervical aponeurosis, roots of the lungs and septum transversum, and the body-wall at the sides on the inner face of the ribs ; behind it passes upwards to below the vertebral column between the lungs and the kidneys, thus completely cutting off the lungs and remains of the pleural cavities above from the air-sacs below, being pierced only by ostia leading from the former to the latter. As a rule striated muscles—costo-pulmonary supplied from corresponding spinal nerves, and sometimes anterior sterno-costal muscles as well—extend from the ribs into the membrane, Figs. 609, 637.

The second longitudinal membrane is the oblique septum of Huxley (diaphragme thoraco-abdominal of Sappey, diaphragmite thoraco-abdominal of Milne-Edwards), attached dorsally to the median mesentery where it meets the pulmonary aponeurosis, and ventrally to the body-wall at or near the edge of the sternum. It may contain unstriated muscle fibres passing forward from the pubis, and extends forwards to the cervical aponeurosis forming the ventral inner wall of the intermediate air-sacs, and backwards to the body-wall as a very thin membrane covering the abdominal sacs. Behind the intermediate sacs the oblique septum meets the post-hepatic septum (see below, p. 639), beyond which in all birds except the *Apteryx* (Owen, 1863 ; Huxley, 911) the abdominal air-sacs project into the intestinal division of the peritoneal cavity. The space between the pulmonary aponeurosis and oblique septum is entirely occupied by the air-sacs, and is not of coelomic origin.

The next partition to be mentioned is the post-hepatic septum, so named by Butler (962-3), who first clearly described its relations and homologies, Figs. 608, 632. It is a transverse membrane stretching obliquely backwards from the oblique septum above to the lateral and ventral body-wall below (Milne-Edwards, 1867; Campana, 894; Weldon, 1883 ; Bignon, 1887–9; Butler, 962 ; Beddard, 953 ; Broman, 959 ; Hochstetter, 969 ; Poole, 974), and is formed of two halves passing outwards from the dorsal mesentery and the ventral mesentery. Dorsally the post-hepatic septum is continuous with the oblique septum and pulmonary aponeurosis, where these combine above the liver and behind the lungs ; this region is distinguished by Butler as the oblique abdominal septum (passing across between the abdominal sacs, and lined on both sides by coelomic epithelium) from the true oblique septum (underlying the thoracic sacs and lined with coelomic epithelium on the ventral side only). Ventrally the post-hepatic septum encloses the
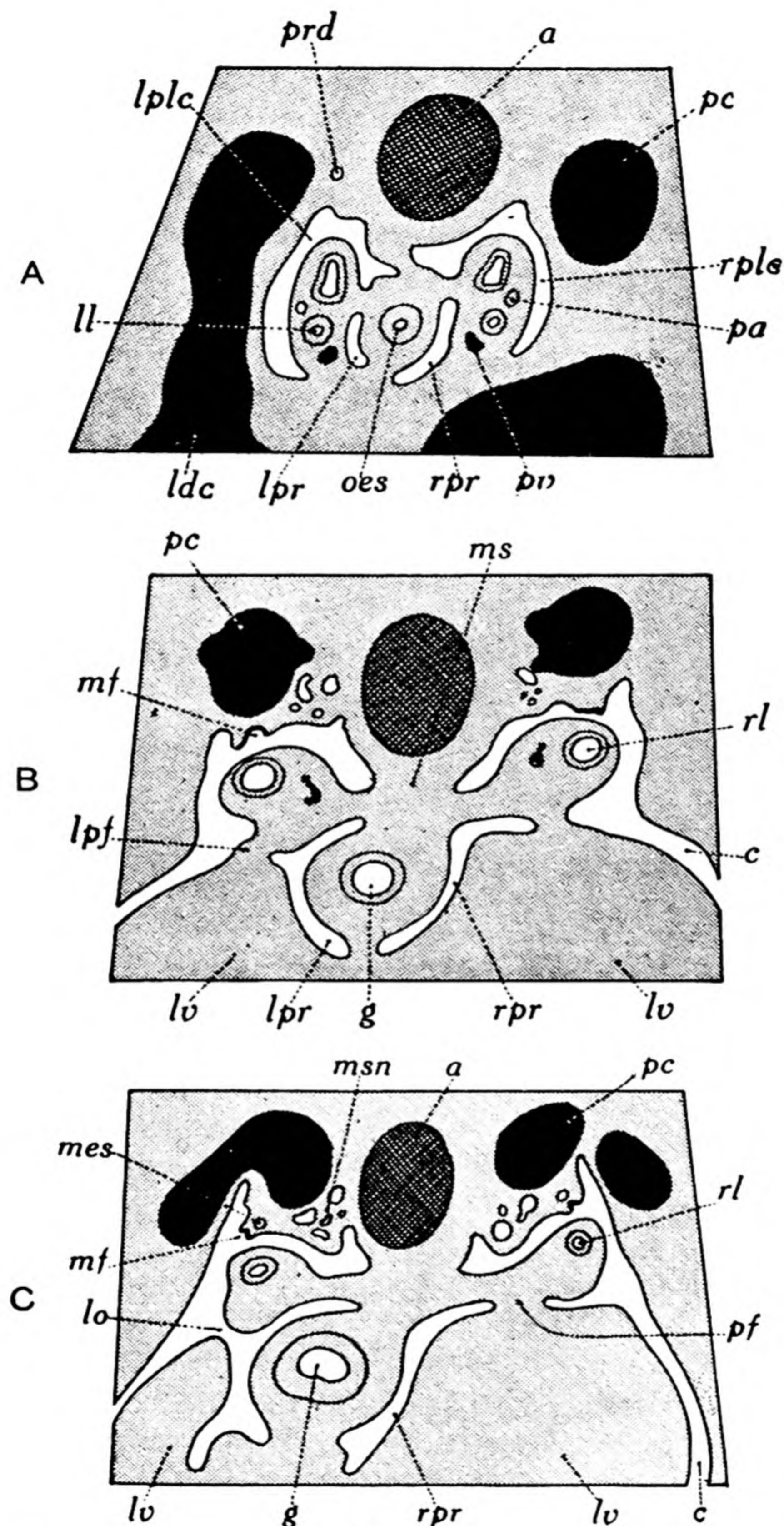
FIG. 633.

Transverse sections of 5-day chick, *Gallus* : A, Most anterior ; C, most posterior.   *a*, Dorsal aorta ; *c*, splanchnocoele ; *g*, gut ; *ldc*, left ductus Cuvieri ; *ll*, left lung ; *lo*, opening of left pulmonary recess ; *lpf*, left pulmonary fold ; *lplc* and *rplc*, left and right pleural coelom still open behind : *lpr* and *rpr*, left and right pulmonary recess ; *lv*, liver ; *mf*, Müllerian funnel ; *mes*, mesonephric duct ; *msn*, mesonephros ; *oes*, oesophagus ; *pa*, pulmonary artery ; *pc*, posterior cardinal ; *pf*, pulmonary fold ; *prd*, pronephric duct ; *pv*, pulmonary vein ; *rl*, right lung.

Passer domesticus, transverse sections of embryo showing development of air-sacs and septa. A, Through anterior thoracic; B, through anterior thoracic; and C, through posterior thoracic. *aas*, Abdominal air-sacs. *aas*, Abdominal sac; *ao*, dorsal aorta; *c*, coelom; *d*, junction of great veins; *g*, gut; *gd*, gizzard; *hl*, hepatic ligament (ventral pulmonary fold); *ll*, left lobe of liver; *lls*, left liver-sac; *lpr*, left pulmonary recess (open in C); *md*, Müllerian duct; *msn*, mesonephros; *nf*, nephric fold; *os*, top of oblique septum; *pc*, pericardial cavity; *pl*, intestinal coelom; *plc*, pleural coelom; *ptc*, liver, sac still continuous with intestinal coelom; *r*, rib; *rl*, right lobe of liver; *rlg*, right lung; *rplc*, right pleural coelom, still open behind; *rpr*, right pulmonary recess; *sg*, spinal ganglion; *sv*, sinus venosus; *sy*, sympathetic ganglion and cord; *uv*, umbilical vein; *vci*, vena cava inferior.

Fig. 634.

gizzard, and thus completes a partition subdividing the original peritoneal coelom into a posterior cavity enclosing the intestine, kidneys, and genital organs, and an anterior cavity enclosing the liver.   Now the latter cavity is further subdivided into four by the complete ventral mesentery reaching the post-hepatic septum, and the third longitudinal membrane which may be called the horizontal hepatic ligament (ventral part of Butler's pulmo-hepatic ligament).   This membrane separates on each side the pneu-
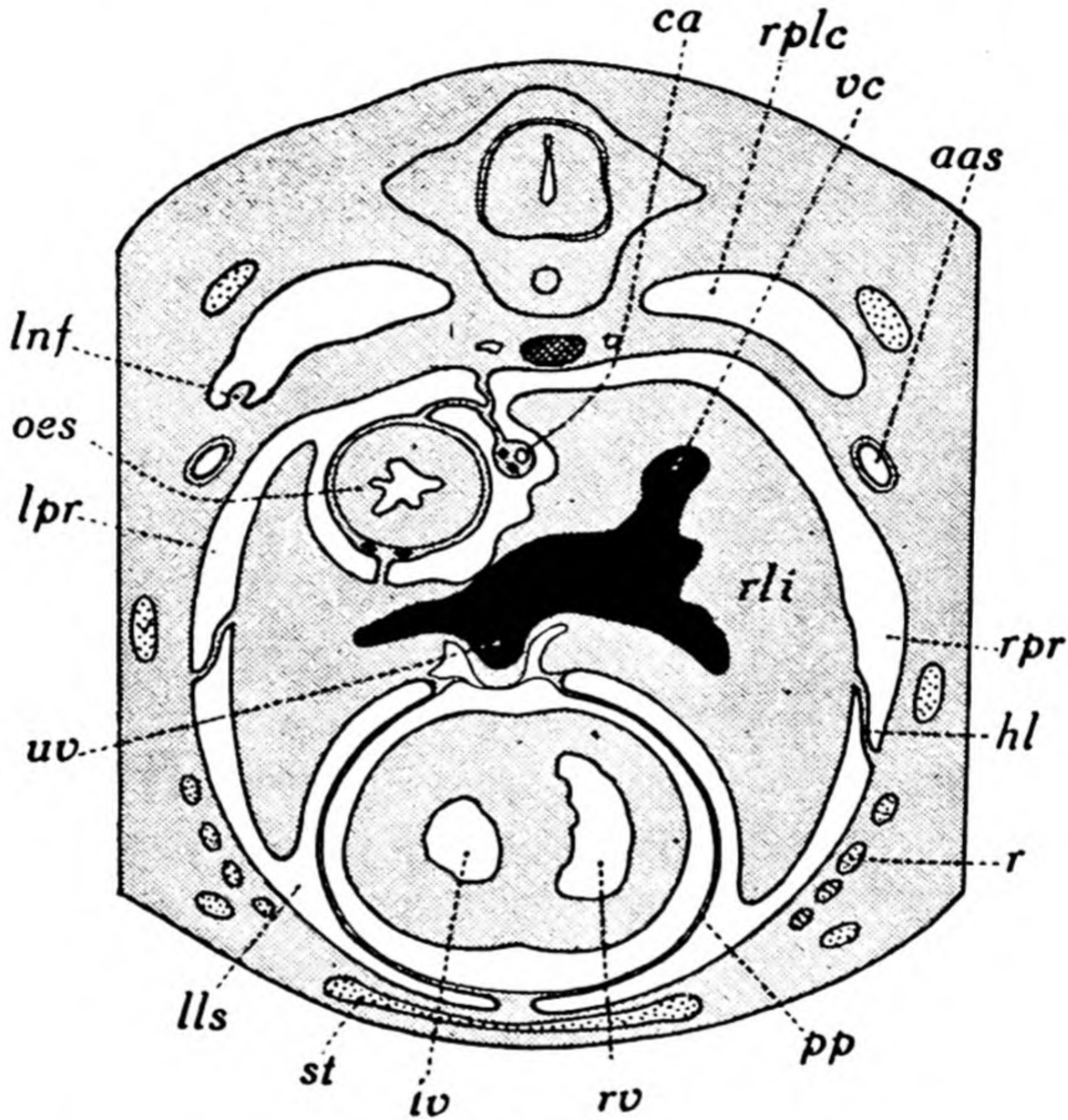
FIG. 635.

Passer domesticus, transverse section of late embryo.   *aas*, Abdominal air-sac ; *ca*, coeliac artery ; *hl*, hepatic ligament (ventral part of pulmonary fold) ; *lls*, left liver-sac ; *lnf*, left nephric fold ; *lpr*, left pulmonary recess ; *lv*, left ventricle ; *oes*, oesophagus ; *pp*, pericardio-peritoneal membrane ; *r*, rib ; *rli*, right lobe of liver ; *rplc*, posterior region of right pleural coelom ; *rv*, right ventricle ; *st*, sternum ; *uv*, umbilical vein ; *vc*, vena cava inferior.

mato-enteric recess above from a ventral cavity into which bulges the liver, the so-called liver-sac of Butler.   While the right pneumato-enteric recess is quite closed by the obliteration of the foramen of Winslow, except in so far as it may open into the left recess by secondary perforation of the median mesentery, this left pneumato-enteric recess may still communicate with the intestinal coelomic chamber by a narrow slit between the gizzard and the body-wall (wall of the left abdominal air-sac), due to the incomplete formation of the post-hepatic septum at this point.

Development of Avian Septa.—The morphology of these avian septa

can only be understood from a knowledge of their development, now fairly complete, thanks to the work of Butler (962), Ravn (977), Hochstetter (835), Bertelli (955), and Poole (974). The development of the septum transversum, studied in detail by Ravn and Brouha (961), differs in no important respect from that described above for the Tetrapods in general. Owing to the backward movement of the heart it becomes very oblique. The median mass, overspreading the anterior face of the liver and passing downwards and backwards into the median hepatic ligament or ventral mesentery, joins the lateral closing folds running down the body-wall from the mesocardia lateralia and
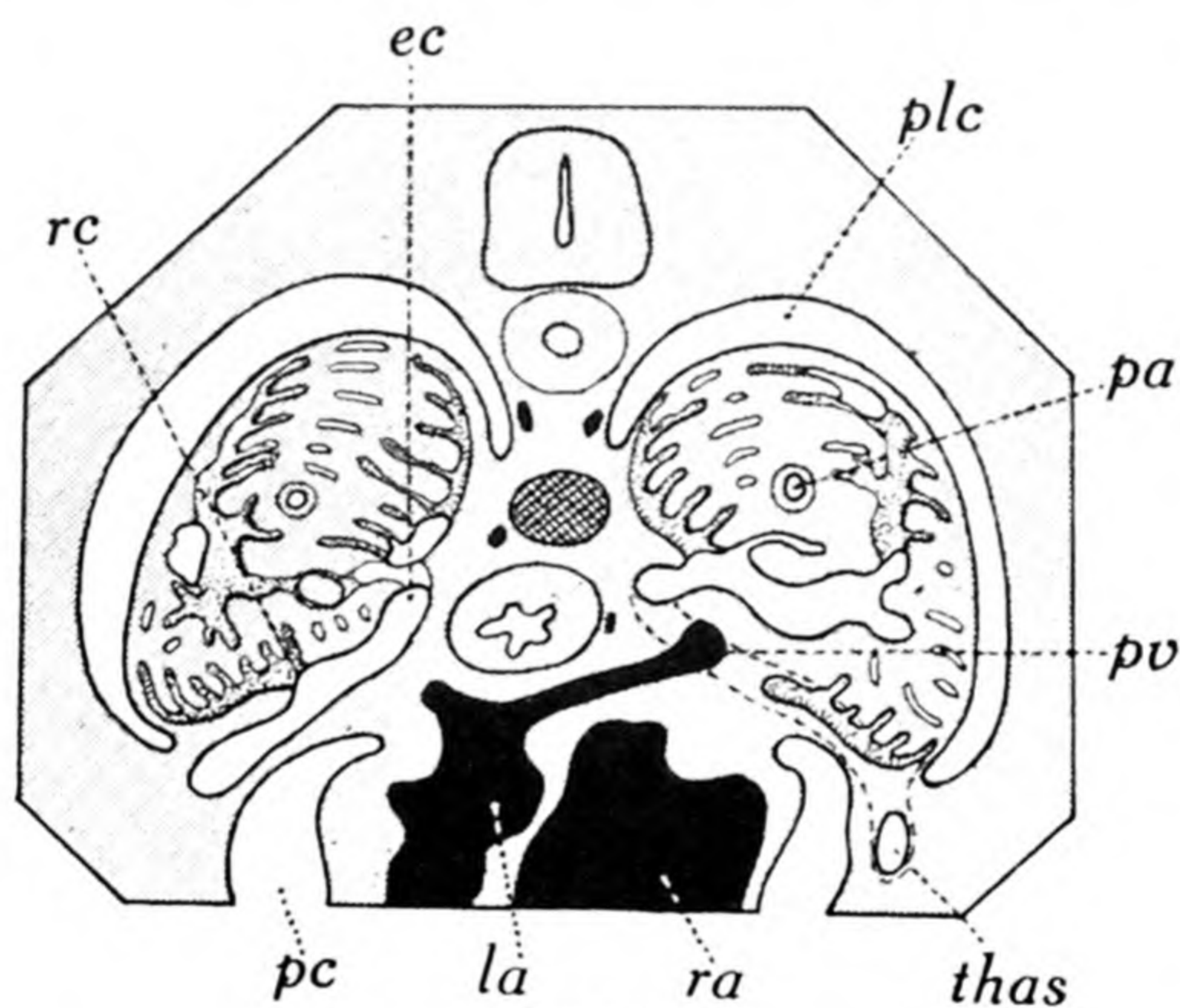
FIG. 636.

Passer domesticus, embryo late stage ; transverse section showing development of anterior thoracic air-sac in pulmonary fold. *ec*, Excurrent bronchus opening into sac ; *la*, left auricle ; *pa*, pulmonary artery ; *pc*, pericardial coelom ; *plc*, pleural coelom ; *pv*, pulmonary vein ; *ra*, right auricle ; *rc*, recurrent bronchus ; *thas*, thoracic air-sac.

enclosing the umbilical veins. Thus, on the eighth day in the chick, the lower coelomic passages are closed. As usual the dorsal passages are closed by the fusion of the ductus Cuvieri with the pulmonary thickenings of the oesophagus, and the pericardium is now shut off by the septum transversum extending over it as a thin pericardio-peritoneal membrane, from which the liver becomes separated off later. The membrane is further increased by the extension forward and downward of the peritoneal cavity (and liver) at the sides of the pericardium. The well-developed and nearly symmetrical pulmonary folds (accessory mesenteries) play an important part in the formation of the avian septa, Figs. 633-7. Forming, of course, the outer walls of the pneumato-enteric recesses, they spread outwards (chick, sixth day) attached to

the edge of the lateral lobes of the liver, and give rise to the floor of the future pleural cavities, into which the lungs project on their dorso-lateral surface. At this stage the pleural cavities still open widely behind, and also by narrow slits at the sides, between liver and body-wall, into the peritoneal cavity. With this cavity the left pneumato-enteric recess communicates by a long aperture in front of the stomach, the ventral region of the pulmonary fold being less developed than the dorsal. On the right side the usual bursa omentalis is developed; but
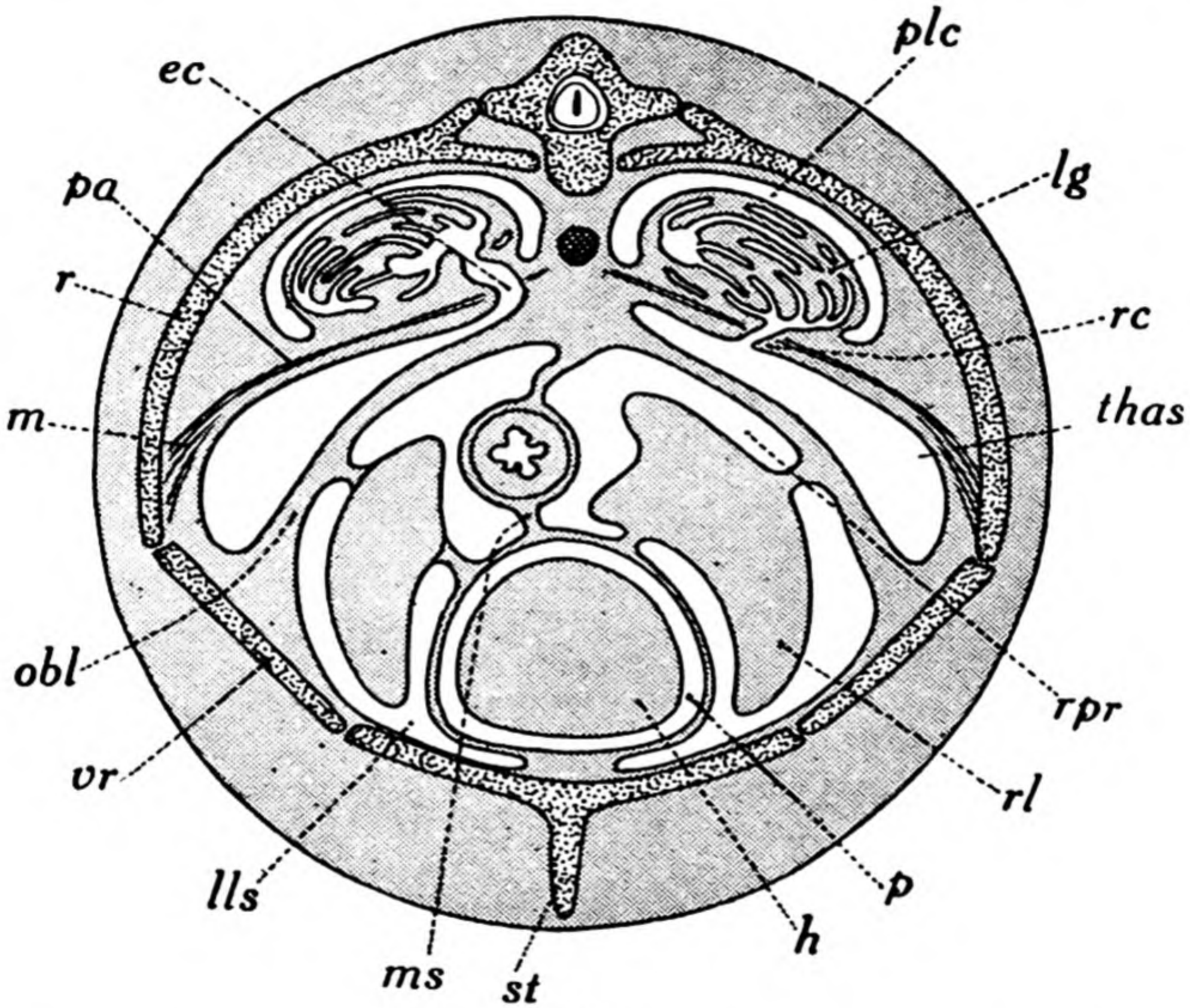
FIG. 637.

Diagram of transverse section through thorax of a Bird. *ec*, Excurrent passage from lung to air-sac through pulmonary aponeurosis; *h*, heart; *lls*, left liver-sac; *lg*, lung; *m*, muscle; *ms*, mesentery below oesophagus; *obl*, oblique septum; *p*, pericardial coelom; *pa*, pulmonary aponeurosis; *plc*, reduced pleural coelom; *r*, dorsal rib; *rc*, recurrent bronchus from sac to lung; *rl*, right lobe of liver; *rpr*, right pulmonary recess; *st*, sternum; *thas*, posterior thoracic air-sac; *vr*, sternal rib.

the primitive foramen of Winslow is closed by the backward growth and fusion of the pulmonary fold, and the bursa omenti majoris may become cut off by fusion of the plica arteriae coeliacae, and subsequently more or less completely obliterated (Butler (962), Broman (959), in *Gallus*).

Meanwhile the pleural cavities become shut off as follows. The pulmonary folds attached ventrally to the liver lobes are stretched out-wards, and fuse progressively from before backwards with the somatic wall. The fusion, starting from the septum transversum, is helped by an ingrowing shelf of the body-wall (E.S.G.), and occurs just below the line

of attachment of the nephric fold, which, however, takes little or no share in the process. In this way the pulmonary fold becomes bent and subdivided into a more dorsal pleuro-peritoneal membrane passing below the lungs to the body-wall, and a more ventral part, the future horizontal hepatic ligament, from the body-wall to the liver. The former is the roof and the latter the ventro-lateral wall of the pneumato-hepatic recess. Thus the pleural coelom above is cut off on each side from the coelomic cavity below destined to become the liver-sac. The pleural cavities become later completely closed behind by the extension backwards of the pleuro-peritoneal membranes which meet posterior closing folds, transverse growths of connective tissue from the median mesentery in front of the kidney and dorsal to the attachment of the pulmonary folds. At this stage, then, the median ventral peri-cardial and two dorsal pleural cavities have been closed off. Later on the lungs press against the ribs, and obliterate the pleural cavities.

In the meantime three paired hollow outgrowths from the bronchi, rudiments of the intermediate and abdominal air-sacs (see p. 600), penetrate into the dorsal region of the pulmonary fold. Here the intermediate sacs expand, growing outwards and downwards, thus splitting the fold into the upper pulmonary aponeurosis and the lower oblique septum (Butler, 963). Between the sacs the tissue is reduced to thin vertical septa. Into the post-pulmonary mass of tissue forming the thickened edge of the pulmonary folds extend the rudiments of the abdominal air-sacs. Each sac becomes applied to and fuses with the lateral abdominal wall, along which it grows. The unsplit portion of the pulmonary folds, stretching between the sacs, the median mesentery and gastric loop of the gut, form that dorsal region of the post-hepatic septum called oblique abdominal septum by Butler (see p. 633).

The development of the ventral region of the post-hepatic septum is difficult to make out. Butler (963), Poole (974), and Hochstetter (969) all derive it wholly or in part from the ventral mesentery. The gastric portion of this mesentery is greatly extended on the left side and fusing with the body-wall binds the stomach to it. The ventral gastric fold thus formed grows up so as to meet the oblique abdominal septum above and the wall of the abdominal air-sac at the side. As mentioned above, a communication remains at this point between the left recess and the intestinal coelom. The right portion of the ventral post-hepatic septum seems to be formed by the lateral and dorsal growth of the free posterior edge of the ventral mesentery along the body-wall, until it meets the oblique abdominal septum.

THE SUBDIVISION OF THE COELOM IN REPTILIA

We naturally turn to the Reptilia for an explanation of the origin of the avian septa. As a rule, in this class the pleural region of the coelom is not shut off from the remainder of the body-cavity; but in the Lacertilia it becomes partially closed owing to the development of a very deep nephric fold, forming a pleuro-peritoneal membrane sometimes attached ventrally to the body-wall as well as the liver, Figs. 628, 631. Hochstetter has also described a vertical posterior closing fold extending from the mesentery behind the tip of the right lung (a vestige of a
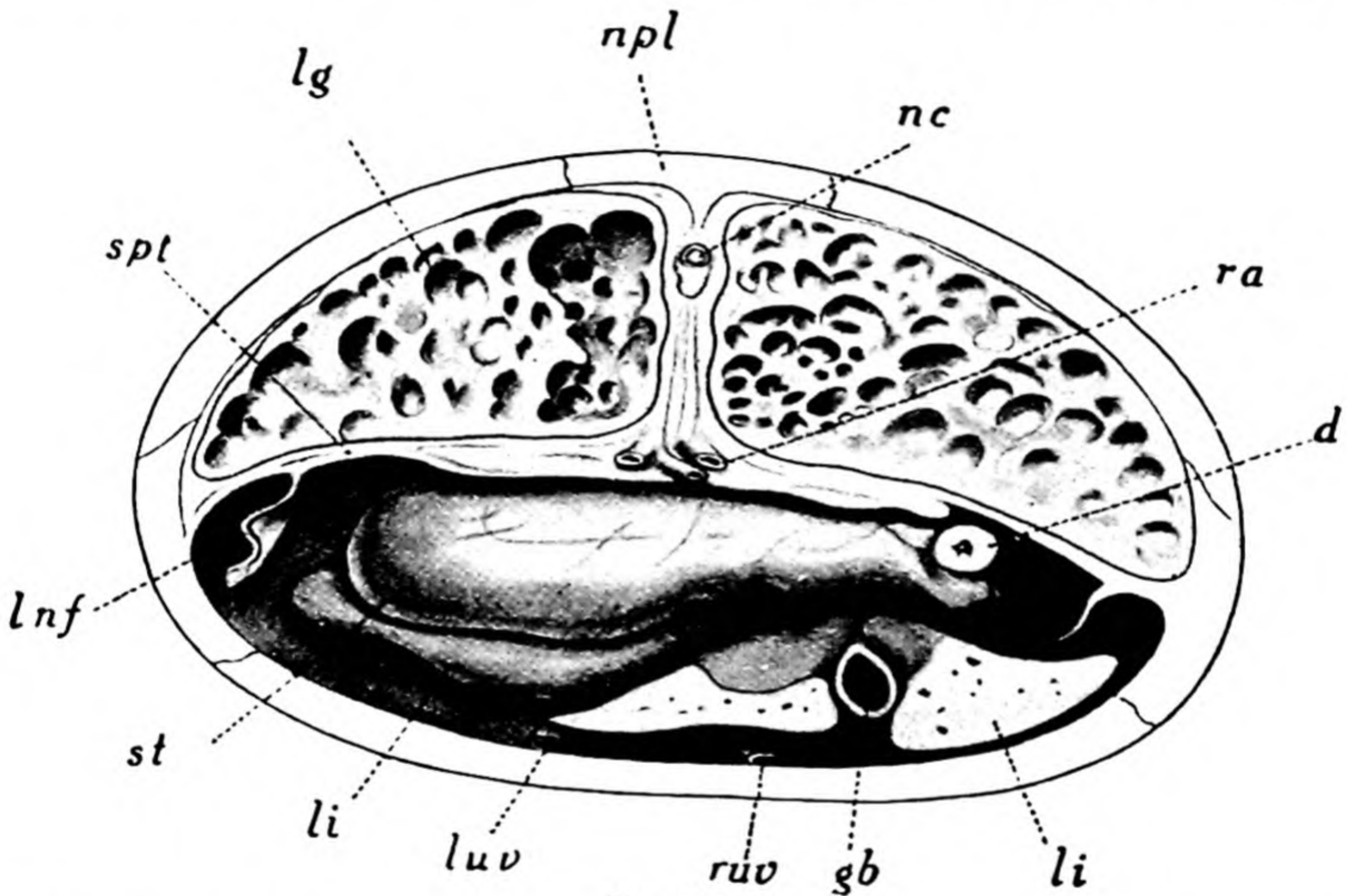
FIG. 638.

Testudo graeca, cut across and seen from behind.   *d*, Duodenum; *gb*, gall-bladder; *li*, liver; *lg*, lung; *lnf*, left nephric fold; *luv*, left umbilical vein; *nc*, nerve-cord; *npl*, neural plate; *ra*, right aortic arch; *ruv*, right umbilical vein; *spt*, septum.

similar fold occurs in some species on the left), which he considers to be homologous with the similar fold found in the embryo of mammals (and birds ?), Fig. 631. When the nephric fold joins the posterior fold, as in *Stellio*, only a narrow aperture of communication remains from the pleural to the peritoneal cavity on the right; in *Agama* even this opening is closed (Hochstetter, 967). Although bearing a certain superficial resemblance to the dorsal diaphragm of the mammal, there can be little doubt that this pleural wall is a special development in the Lacertilian. With the oblique septum of the bird it, of course, has no connexion. On the other hand, in the Varanidae, where the pleural cavity is obliterated and the lungs are pressed up against the vertebral column and ribs, there is a membrane

extending from the body-wall and covering the lungs below somewhat as in birds; but there is no evidence that it is really derived from the pulmonary folds. In the Chelonia, however, the lungs adhere to the body-wall above, and are partially (*Emys*) or entirely (*Testudo*) shut off from the peritoneal cavity by a septum which, according to Bertelli, is developed by the spreading outwards and fusion with the body-wall of the pulmonary folds, just as in birds, Fig. 638. These conditions deserve further study.

It is in the Crocodilia, which as Huxley maintained are of all living reptiles the most closely allied to birds, that we might expect to find the avian septa developed; and in the Crocodile, indeed, there is a complete post-hepatic septum shutting off pleural cavities, pulmo-hepatic cavities, and liver-sacs from an intestinal chamber behind (Huxley, 911; Butler, 962; Poole, 974; Hochstetter, 969). Nevertheless, the pleural cavity is held by Butler and Hochstetter not to correspond strictly to that of birds, since it appears to be cut off from the ventral liver-sac by the adhesion of the liver lobes to the body-wall (ventral oblique hepatic ligament), and not by the lateral fusion of the pulmo-hepatic liga-

Fig. 639.

View from behind of post-hepatic septum of *Crocodilus niloticus* (from Hochstetter, 1906). *acm*, Coeliaco-mesenteric artery; *ao*, dorsal aorta; *she*, limit of saccus hepato-entericus (left pulmonary recess), and *shpe*, of right saccus hepatopulmoentericus (right pulmonary recess) seen through septum; *st*, section of stomach; *vad*, right anterior abdominal vein; *vas*, left anterior abdominal vein; *vci*, vena cava inferior.

ment. A short fold passing inwards from the ventral body-wall between the liver and the lung is supposed to represent a rudiment of the 'avian diaphragm' (Butler, 962). Yet it seems not impossible that the ventral oblique hepatic ligament really represents the outer region of the pulmo-hepatic ligament which has shifted downwards, in which case the septa and cavities of the Crocodile would correspond almost exactly with those of a bird, excepting, of course, for the absence of air-sacs, Figs. 639, 640.

As for the origin of the post-hepatic septum itself, Butler has shown that it exists in an incomplete state in the family Tejidae alone among Lacertilia. In *Tupinambis*, for instance, two folds diverge right and left from the hinder margin of the ventral mesentery; they are attached to the ventral and lateral body-wall, and have a free dorsal edge bounding a small opening on the left and a larger on the right, communications

between the pleural and the intestinal regions of the coelom. Were these folds completed dorsally, the crocodilian condition would be realised; while, on the contrary, were they less developed, the condition found in most Lacertilia would result.

Butler has described a complete post-hepatic septum in the Ophidia, whereby two liver-sacs are closed off (the pleural cavities, and apparently also the pulmo-hepatic recesses, disappear in development).
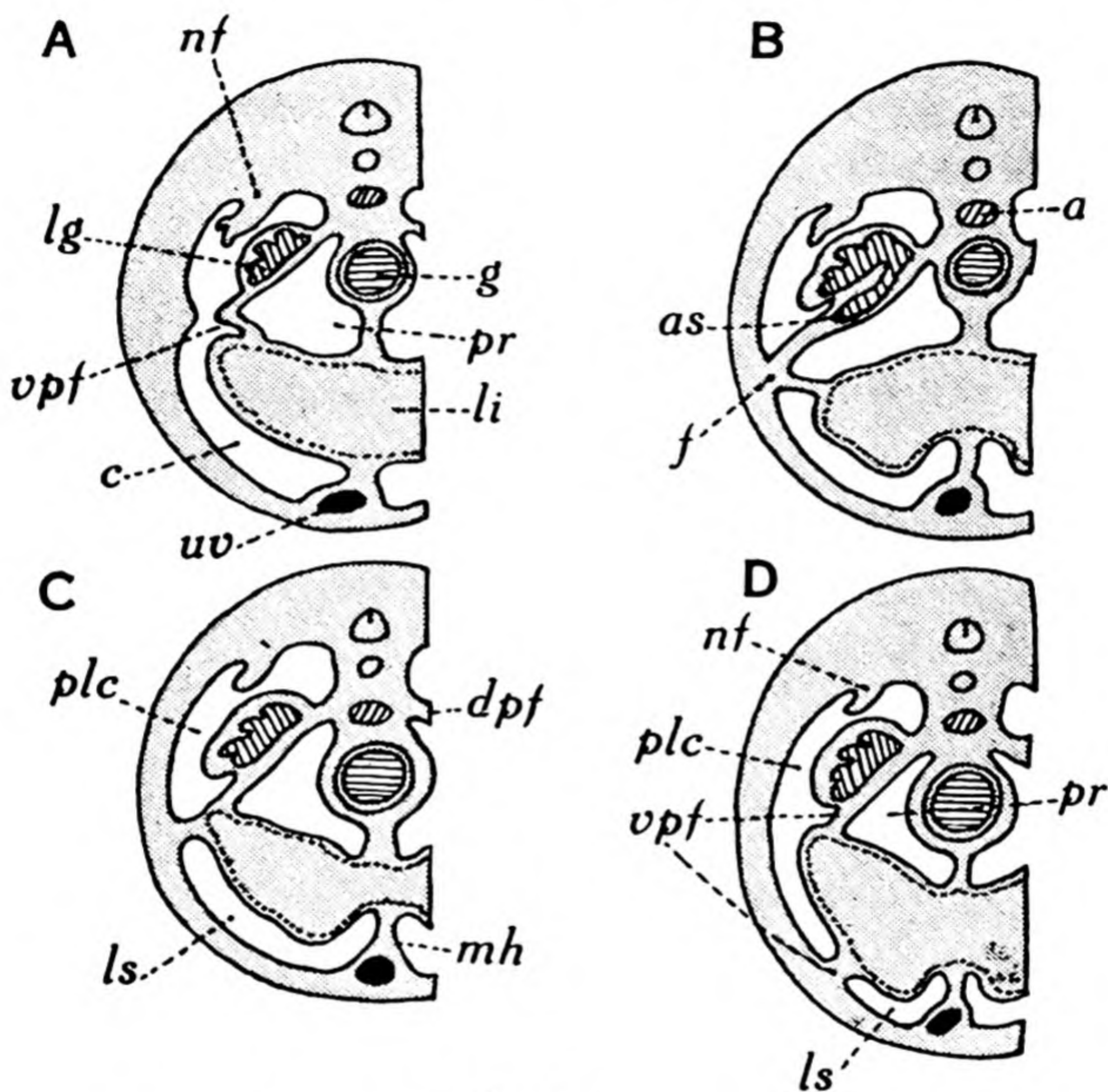
FIG. 640.

Diagrams illustrating development of coelomic septa in a bird, A and B, and a crocodile, C and D. A, early, and B, later stage; C, stage corresponding to B; D, nearly adult. *a*, Dorsal aorta; *as*, air-sac; *c*, splanchnocoele; *dpf*, dorsal pulmonary fold; *f*, fusion of ventral pulmonary fold with body-wall; *g*, gut; *lg*, lung; *li*, liver; *ls*, liver-sac; *mh*, hepatic ligament or ventral mesentery; *nf*, nephric fold; *plc*, pleural coelom; *pr*, pulmonary recess; *uv*, umbilical vein; *vpf*, ventral pulmonary fold.

While the post-hepatic septum of the Crocodilia may be considered as homologous with that of Aves (although Hochstetter does not admit its full homology), it is difficult to account for the appearance of this septum in the Tejidae and Ophidia. Since it is absent in other Lacertilia and in *Sphenodon* it can hardly be considered as a primitive structure, and we are left with the unsatisfactory conclusion that it has been independently developed in two or more groups.

THE MAMMALIAN DIAPHRAGM

The development of the mammalian diaphragm is brought about by a very complicated process difficult to describe, partly owing to its being built up from several separate rudiments, partly from its connexion with the vascular system, and liver, and partly from the constant relative shifting of its parts and the associated organs during ontogeny, and the difficulty of representing, in three dimensions, the various curved surfaces involved except by means of models. Our modern knowledge of its development may be said to date from the work of Uskow on the rabbit (979). Lockwood (971), Ravn (975-7), Bertelli (954), Mall (972), Broman (960), and especially Brachet (957-8), have confirmed and completed his account.

Very early, when the embryo is scarcely folded off from the extra embryonic layers, the mesocardium laterale appears, owing to the splanchnic meso-blast covering the omphalomes-enteric veins meeting the somatic wall, and the ventral pericardio-peritoneal passage is almost at once obliterated, Figs. 641-642, 645. A complete ventral septum transversum is thus early formed just in front of the anterior intestinal portal, from which it soon becomes separated owing to the narrowing of

FIG. 641.

Reconstruction of embryo *Sus*, domestic pig, 5 mm. long, cut transversely through sinus venosus, *sv*, and seen from behind. *a*, Lateral aorta ; *dc*, ridge en-closing ductus Cuvieri; *ldc*, entrance of left ductus; *lpf*, left pulmonary fold ; *oes*, oesophagus ; *p*, peri-toneal coelom ; *pc*, posterior cardinal ; *pl*, wall of future pleural cavity ; *plp*, pleuro-pericardial passage still widely open ; *rdc*, entrance of right ductus Cuvieri ; *rpf*, right pulmonary fold ; *rpr*, right pulmonary recess ; *st*, septum transversum.

the yolk-stalk and growth of the liver. As the latter organ enlarges spreading over the posterior surface of the septum towards the body-wall laterally and ventrally, the septum shifts not only backwards but also into a more upright position. At first, while its dorsal free edge, delimiting the dorsal pleuro-pericardial passages (ductus pleuro-pericardiacus and recessus parietalis dorsalis of His) on either side of the mesentery, is occupied by the ductus Cuvieri, the paired and symmetrical umbilical and omphalomesenteric veins reach the sinus venosus through the septum transversum (that dorsal region of it which represents the mesocardia

lateralia). Later, the umbilical veins lose their anterior connexions, and the vena cava inferior alone pierces the septum from behind, combined in the embryonic stages with the ductus venosus Arantii.

The development of the pleuro-pericardial membrane, destined to close off the pericardium below from the pleural cavities above and at the sides, takes place owing to the backward shifting of the heart and forward growth of the pleural cavities by the extension of that dorsal region of the septum transversum which is not invaded by the liver. The ductus Cuvieri play an important part in the development of the membrane and the closure of the dorsal coelomic passages or pleuro-pericardial communi-
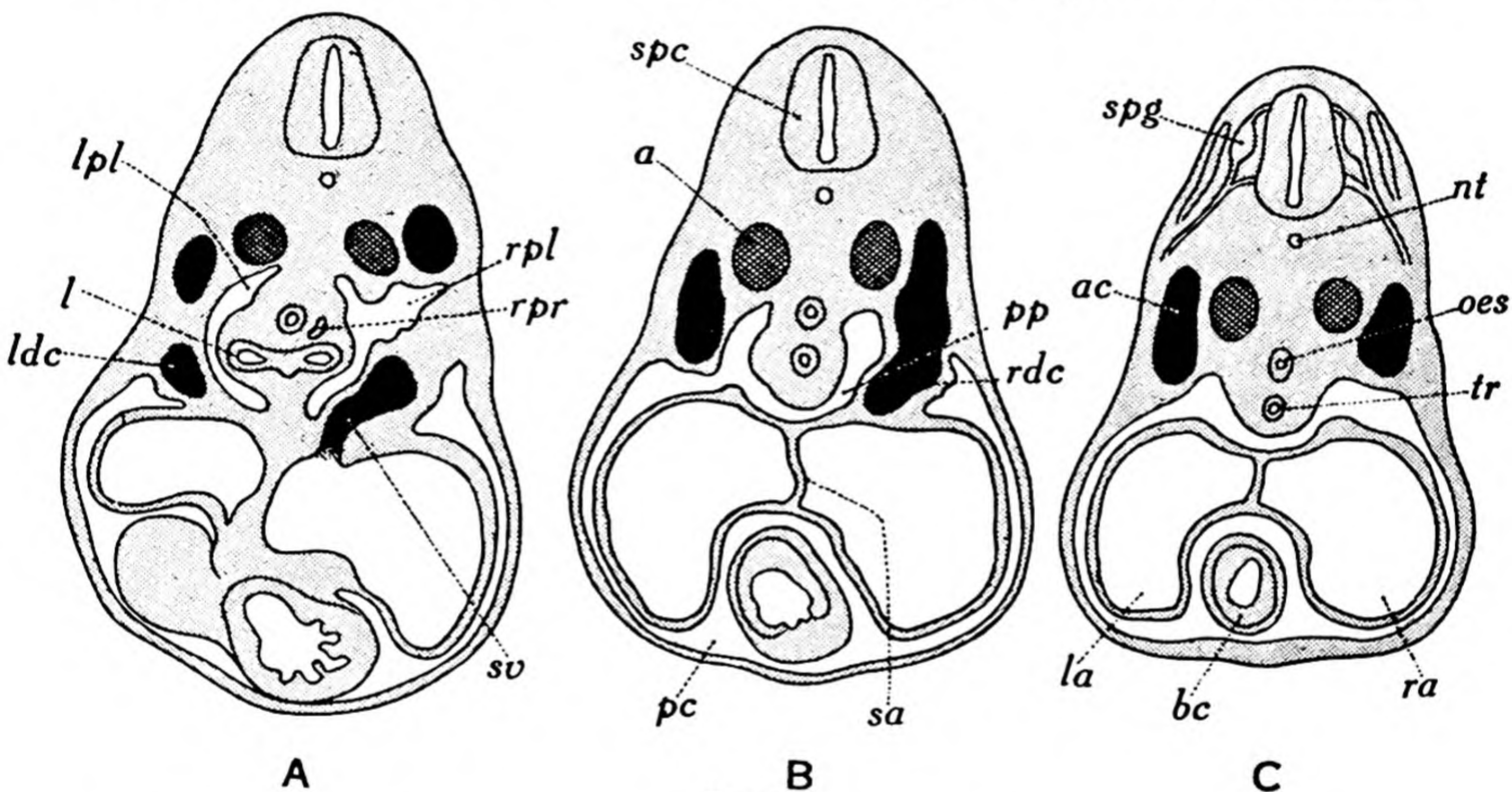
FIG. 642.

Transverse sections through pericardial region of embryo *Sus*, domestic pig, 5 mm. long. C, Most anterior; A, most posterior. *a*, Lateral aorta; *ac*, anterior cardinal; *bc*, bulbus cordis; *l*, lung bud; *la*, left auricle; *ldc*, left ductus Cuvieri; *lpl*, left pleural coelom; *nt*, notochord; *oes*, oesophagus; *pc*, pericardial coelom; *pp*, passage from pericardial to pleural cavities; *ra*, right auricle; *rdc*, right ductus Cuvieri; *rpl*, right pleural coelom; *rpr*, right pulmonary recess; *sa*, septum atriorum; *sv*, sinus venosus; *tr*, trachea.

cations. At first these veins run in the dorsal free edge of the septum transversum outwards and upwards in the body-wall; then, as the heart passes backwards, they lengthen and bend forwards, taking up a position more and more parallel and relatively nearer to the oesophagus and trachea as the pleural cavity expands. Thus the upper part of the septum becomes stretched out, so to speak, as a thin pleuro-pericardial membrane between the inner ductus Cuvieri, the outer body-wall, and the ventral region of the septum transversum attached to the liver. In this way is formed a membranous floor to the pleural cavity passing transversely and obliquely forwards and upwards. In early stages a pleural groove

extends on either side of the mesentery forwards on to the roof of the pericardium ; the pleuro-pericardial passage over the transverse septum becomes converted into a narrow slit between the ductus Cuvieri and the pulmonary ridges or masses of splanchnic mesoblast into which grow the lung-buds. These slits close from before backwards, leaving for a considerable time two minute pleuro-pericardial canals, Fig. 650, comparable
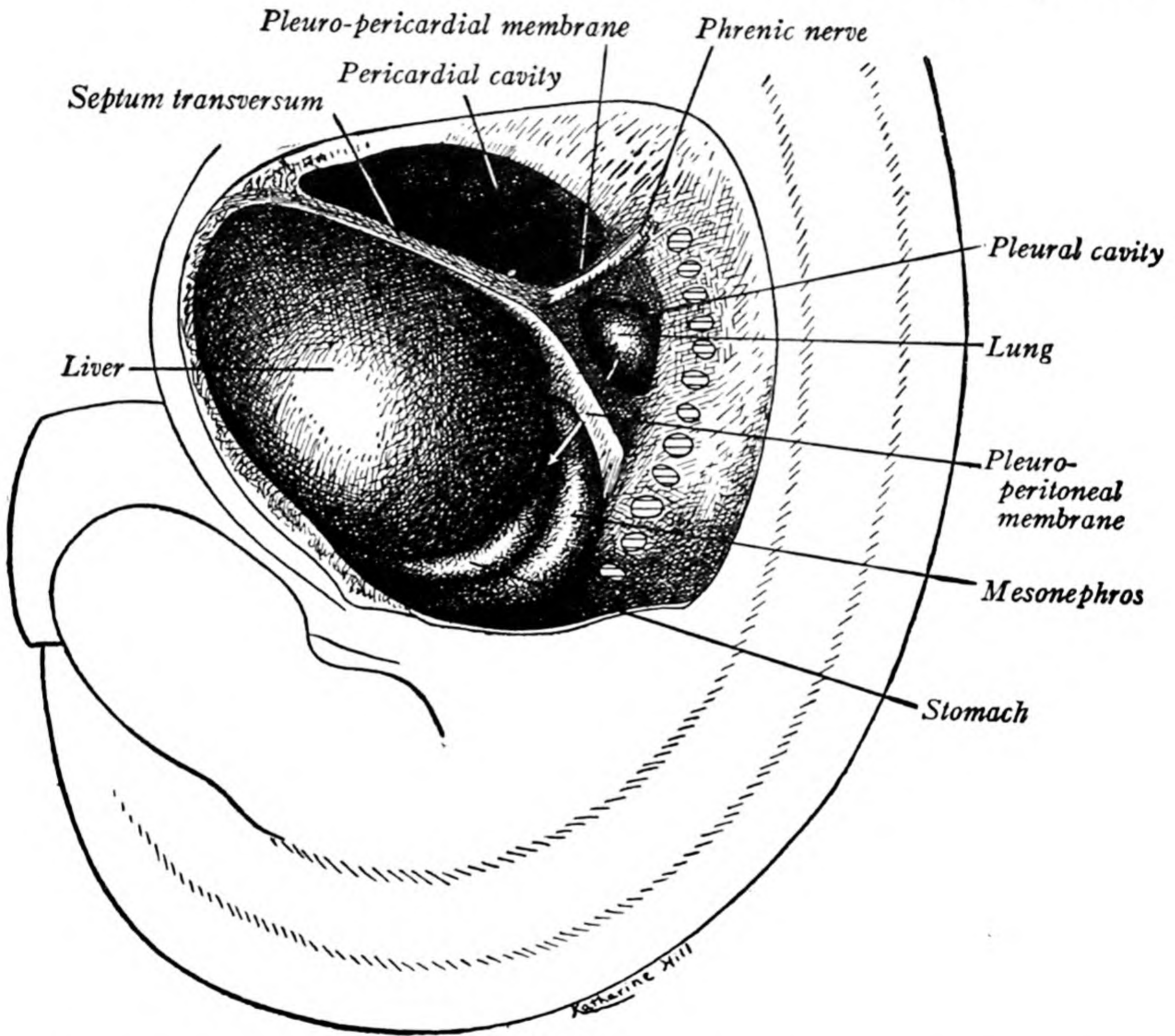
FIG. 643.

Reconstruction of 11 mm. human embryo to show development of diaphragm (from Prentiss and Arey, *Text-book of Embryology*, 1917).

to the permanent pericardio-peritoneal canals of the Elasmobranch, p. 619. Although these canals appear to be finally obliterated, they may occasionally persist open as abnormalities. The ductus Cuvieri have now sunk below the membrane to reach the sinus venosus, and to the fusion of them and the oesophagus with the sinus is due the final closure of the canals. Thus is completed the floor of the anterior region of what we may call the primitive pleural cavity. There remains to be described the develop-

ment of the very important phrenic nerve. It appears early, when the
septum is situated about the level of the fifth cervical ganglion, as a
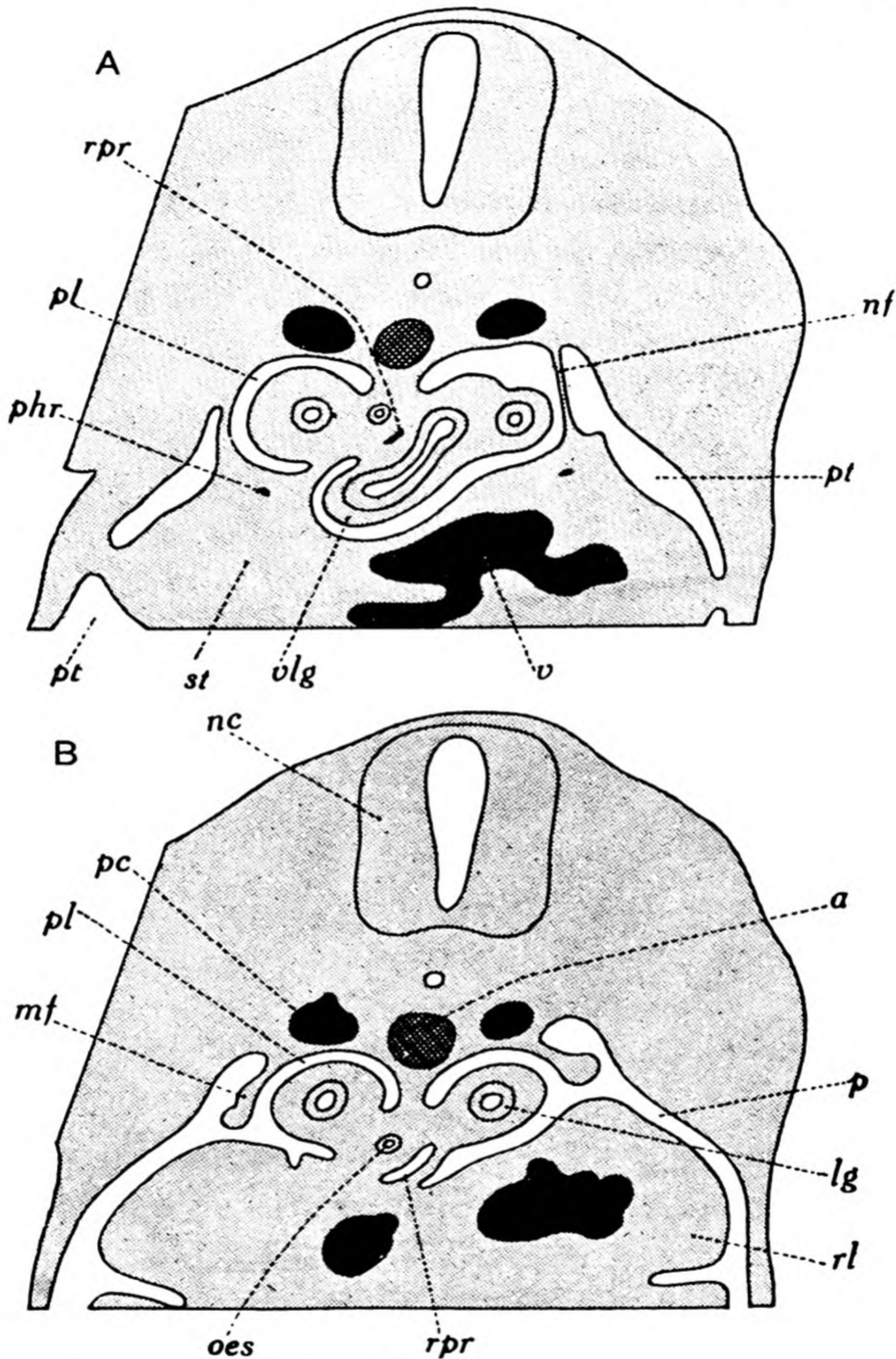
FIG. 644.

Mus musculus, transverse sections of embryo. A more anterior than B. *a*, Dorsal aorta ; *mf*,
Müllerian funnel ; *nf*, nephric fold (pleuro-peritoneal membrane) ; *oes*, oesophagus ; *p*, peritoneal
coelom opening into pleural coelom ; *pc*, post-cardinal ; *pt*, peritoneal coelom ; *phr*, phrenic nerve ; *pl*,
left pleural coelom ; *rl*, right lobe of liver ; *rpr*, right pulmonary recess ; *st*, septum transversum
on liver ; *v*, vein ; *vlg*, ventral lobe of right lung.

compound nerve formed from branches of the third, fourth, and fifth
cervical nerves passing down outside and behind the ductus Cuvieri to

the dorsal region of the septum. When the ductus Cuvieri lengthens as the heart recedes, the nerve stretches back at first obliquely, then almost longitudinally, in the pleuro-pericardial membrane to its insertion in the septum transversum. The latter connexion remaining constant forms an important topographical point when comparing the embryonic septum with the adult diaphragm, Figs. 643, 646, 649, 650.

The shutting off of the hinder region of the pleural cavities is brought about by the combination of three structures. The floor is formed from a thick layer of mesoblast (dorsal diaphragm of Uskow) overlying the liver and apparently derived partly from the mesentery between it and
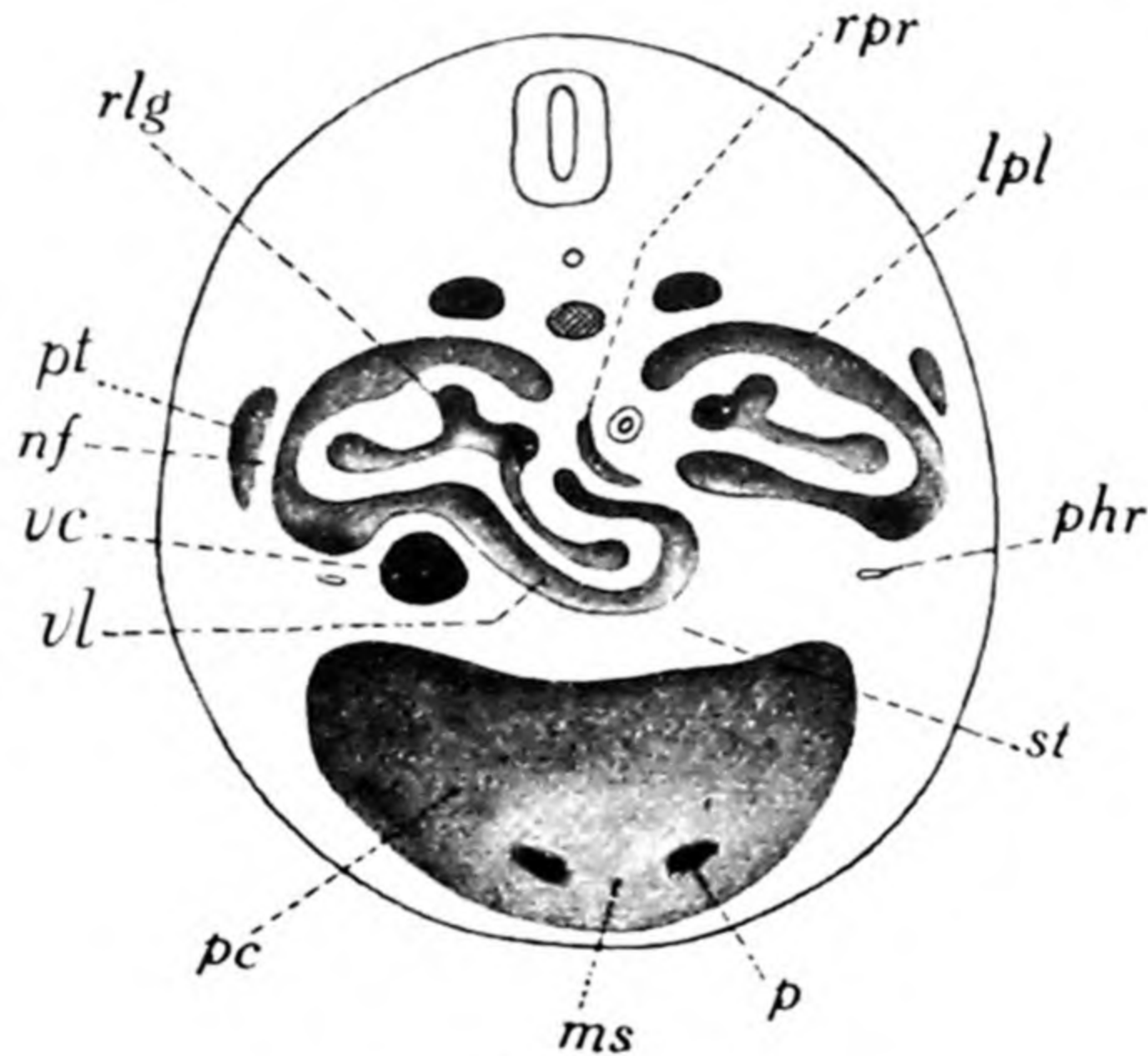
FIG. 645.

Diagrammatic reconstruction of embryo mouse, *Mus musculus*, before complete closure of peri-cardial cavity. Anterior view of embryo cut transversely through pericardial coelom, *pc. lpl,* Left pleural coelom ; *ms,* ventral mesentery ; *nf,* nephric fold ; *p,* passage from pericardial to peri-toneal cavities ; *phr,* phrenic nerve ; *pt,* abdominal or peritoneal coelom ; *rlg,* right lung ; *rpr,* right pulmonary recess ; *st,* septum transversum ; *vc,* vena cava inferior ; *vl,* ventral diverticulum of pleural cavity.

the gut (lesser omentum, gastro-hepatic mesentery), but mostly from a backward growth of the dorsal edge of the septum transversum itself, as is evidenced by the course of the dorsal branch of the phrenic nerve. This floor, passing obliquely backwards and upwards, forms an angle with the pleuro-pericardial membrane as it meets it on the top of the septum transversum, Fig. 643.

The second element contributing to the pleural wall is the pleuro-peritoneal membrane, derived from the nephric fold, Figs. 644, 646-7. It first appears as a dorsal ridge continuous with the meso-nephric fold behind, and running down the posterior surface of the ductus Cuvieri to the dorsal edge of the transverse septum, and so on to the lateral lobe of the liver, where it merges with the outer edge of

the mesoblastic layer on the floor of the pleural cavity described above. From the vertical part of the ridge the pleuro-peritoneal membrane develops, and its dorsal and ventral extensions are known as its dorsal and ventral pillars (Uskow, 979). As the ductus Cuvieri bends forwards, the nephric fold remains behind attached to the body-wall, growing backwards as an almost vertical (sagittal) membrane,
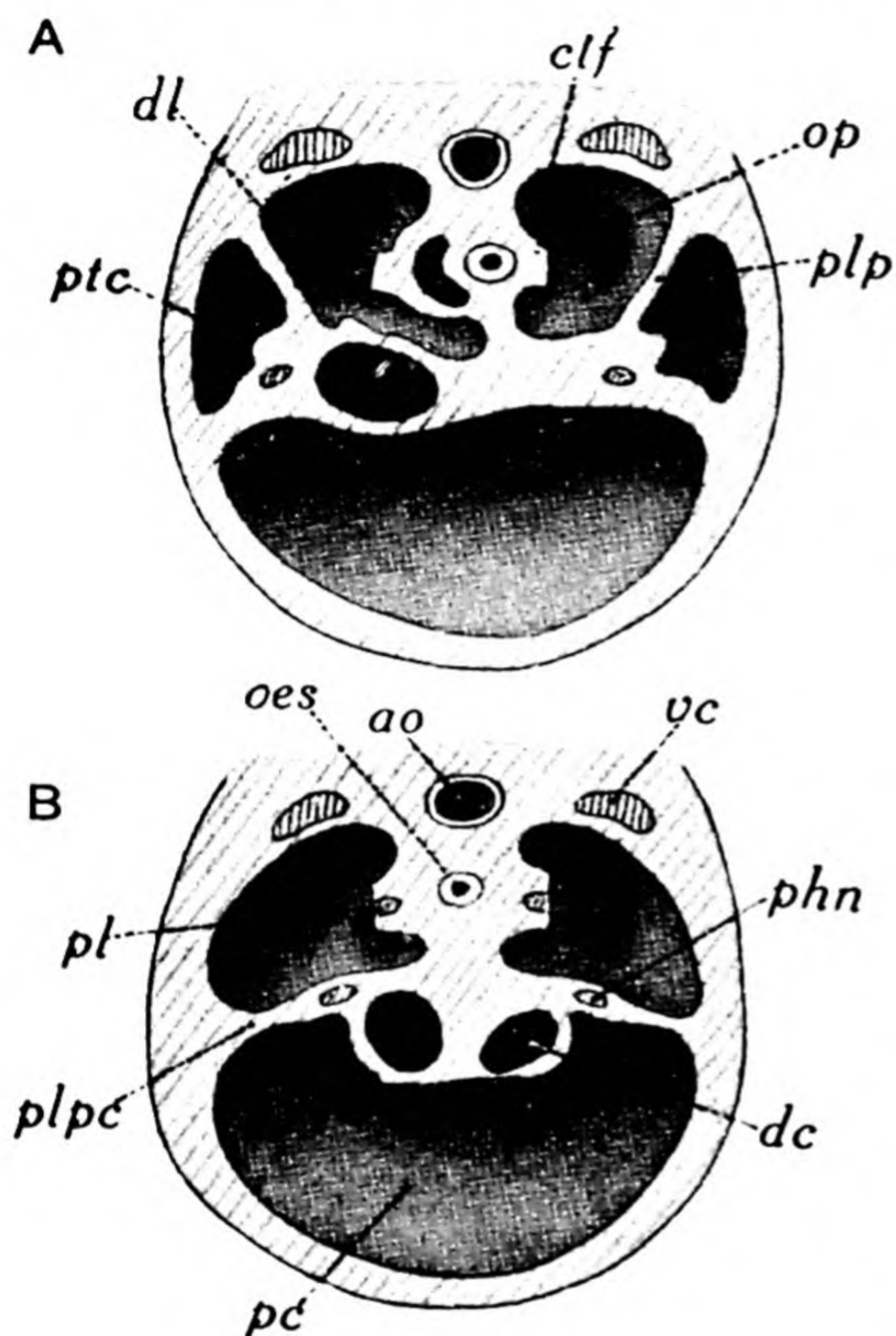
FIG. 646.

Diagrams of *embryo Mammal* cut transversely through pericardial and pleural cavities, A, and more posteriorly, B; anterior view, lungs and heart removed. *ao*, Dorsal aorta; *clf*, left posterior closing fold; *dc*, ductus Cuvieri; *dl*, tissue overlying dorsal surface of liver; *oes*, oesophagus; *op*, opening from left pleural to peritoneal coelom; *pc*, pericardial coelom; *phn*, phrenic nerve; *pl*, cut surface of fold supporting lung; *plp*, pleuro-peritoneal membrane; *plpc*, pleuro-pericardial membrane; *ptc*, peritoneal coelom; *vc*, cardinal vein.

with a free posterior margin; it thus tends to separate an inner pleural chamber above the liver from an outer peritoneal recess, opening behind and below into the general peritoneal cavity. The extent to which the recess is developed, extending over the pericardium, seems to vary considerably in different mammals; and appears to be of little morphological importance, being later on flattened out, so to speak, and merged with the general peritoneal space behind the diaphragm. In Marsupials (*Trichosurus*, E.S.G.) the recess is small; but in those forms like the Rabbit (Uskow and Brachet) or Guinea-pig (Hochstetter, 835), where it is large, the base of the pleuro-peritoneal membrane marks off an inner pleuro-pericardial from an outer peritoneo-pericardial membrane. Both the dorsal and the ventral pillars of the nephric fold tend to approach the middle line behind, and the growing pleuro-peritoneal membrane narrows the originally wide communication of the pleural coelom with the peritoneal coelom to a small posterior slit. But the final closure of the pleural cavity is brought about on the right side by the fusion with the pleuro-peritoneal membrane of a transverse outgrowth of the pulmonary fold, bearing a cup-like depression to receive the tip of the lung. On

the left side the membrane meets a similar outgrowth (posterior closing fold) from the dorsal mesentery, Figs. 646-7, 649, 650.

FIG. 647.

Mus musculus, rather late embryo, before complete closure of pleural cavities. Reconstruction cut transversely and showing from in front posterior ends of nephric folds, etc. *da*, Dorsal aorta; *li*, liver; *msn*, mesonephros; *nf*, nephric fold; *pc*, posterior cardinal; *pt*, peritoneal coelom; *rppf*, right posterior closing fold; *rpr*, right pulmonary recess; *st*, septum transversum; *vc*, vena cava inferior.

This closure of the pleural cavity takes place at a comparatively late stage; meanwhile the pleuro-peritoneal membrane, at first almost sagittal in position, has become flattened out and extended laterally, and moulded on the concave surface of the liver to acquire its definitive shape as the dorsal region of the diaphragm. At the same time still greater changes take place in front, where the small
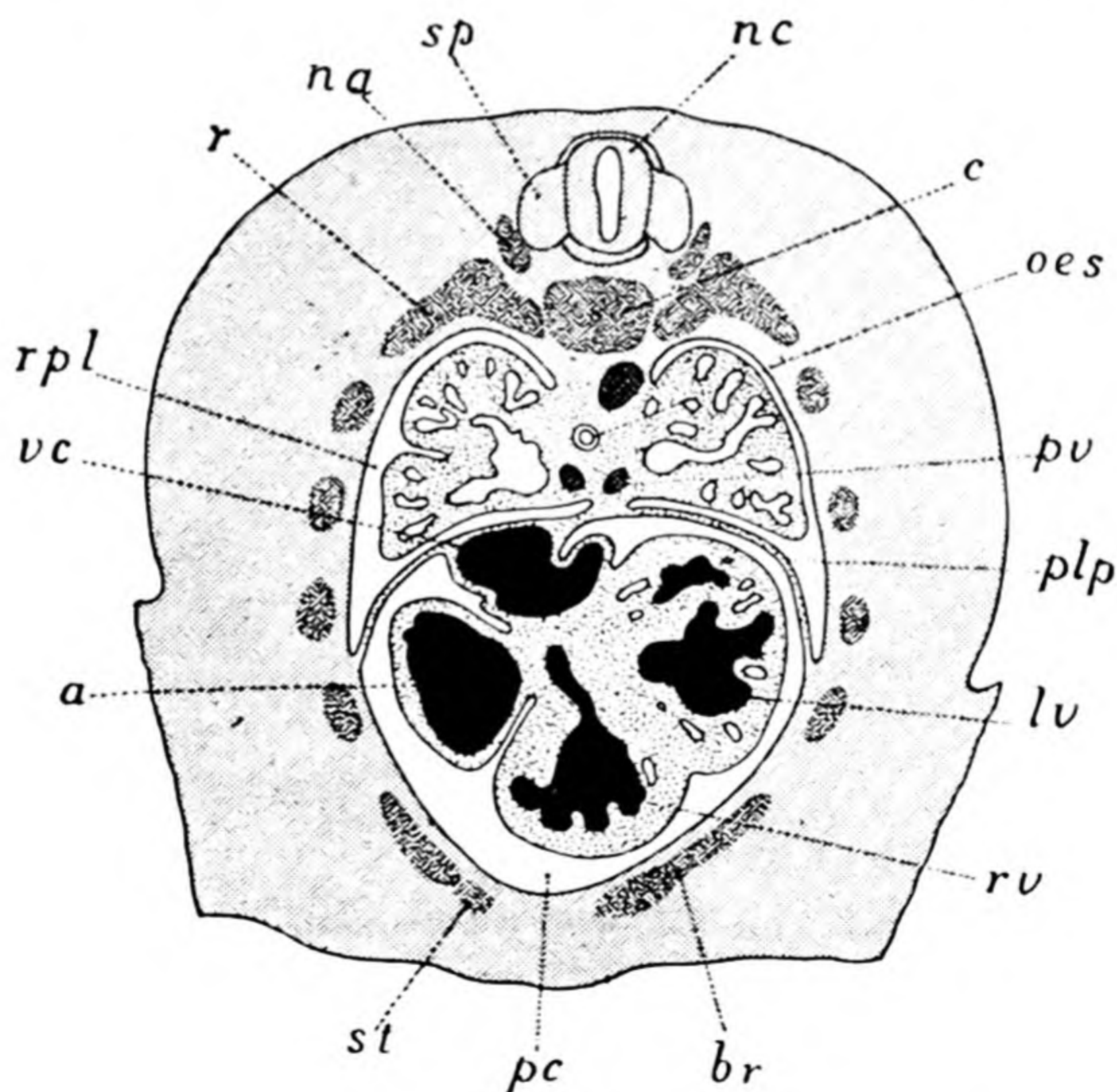
FIG. 648.

Trichosurus vulpecula, embryo 10 mm. long; transverse section of thorax. *a*, Auricle; *br*, sternal rib; *c*, centrum; *lv*, left ventricle; *na*, neural arch; *nc*, nerve-cord; *oes*, oesophagus; *pc*, peri-cardial coelom; *plp*, pleuro-pericardial membrane; *pv*, pulmonary vein; *r*, rib; *rpl*, right pleural coelom; *rv*, right ventricle; *sp*, spinal ganglion; *st*, sternal band; *vc*, vena cava inferior.

primitive pleural cavity expands rapidly outwards and downwards, carrying the outer margin of the pleuro-pericardial membrane ventrally, until in some cases it almost meets that of the opposite side below the heart.　By the ingrowth of the coelomic epithelium at the sides the liver also becomes peeled off from the diaphragm, remaining attached to it by the gastro-hepatic mesentery above, the coronary ligaments at the sides, and the falciform ligament below, Figs. 651-3.

During this process a great expansion of the diaphragm takes place
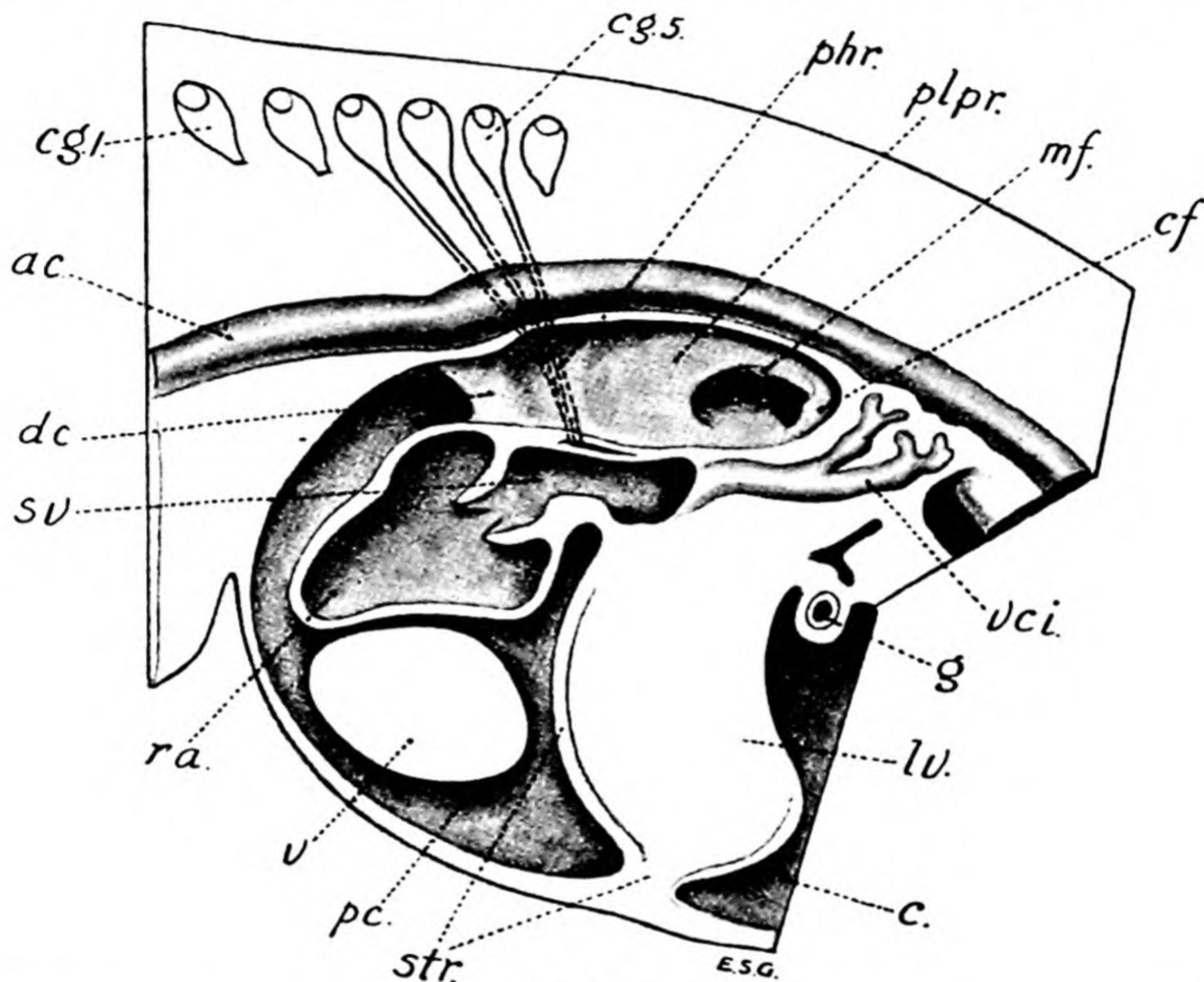
FIG. 649.

Mus musculus, 12-day embryo ; pericardial region cut longitudinally to right of middle line ; inner view of right side, reconstructed. ac, Anterior cardinal ; c, abdominal (peritoneal) coelom ; cf, posterior closing fold ; cg1-5, cervical ganglia ; dc, ductus Cuvieri in transverse septum ; g, gall-bladder ; lv, liver ; mf, Müllerian funnel on nephric fold ; pc, pericardial coelom ; phr, phrenic nerve ; plpr, pleuro-peritoneal membrane (nephric fold) ; ra, right auricle ; str, septum transversum ; sv sinus venosus ; v, wall of ventricle ; vci, vena cava inferior.

at the sides.　How much of this new membrane between the peritoneal and pleural cavities is derived from the body-wall and pleuro-peritoneal membrane respectively, it is difficult if not impossible to say.　According to Brachet, the greater part of it would be of pleuro-peritoneal origin ; but there appears to be no good evidence that this membrane spreads down into the ventral region of the diaphragm.　Rather would the ventral half of the diaphragm appear to be derived almost entirely from the body-wall and transverse septum, as indicated in the diagram, Fig. 654, showing the final constitution of the mammalian diaphragm.　　•
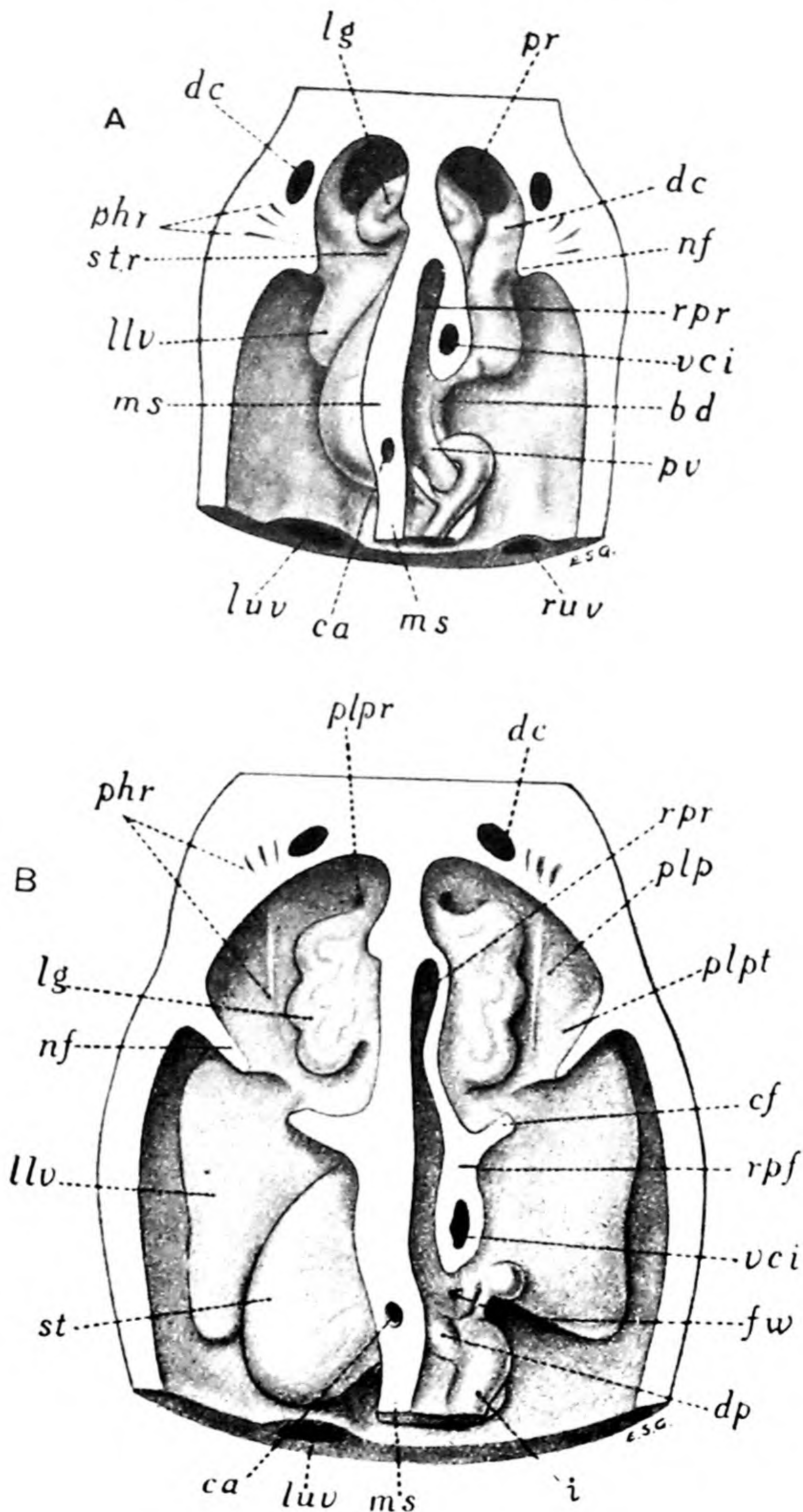
FIG. 650.

Diagrams of anterior trunk region of embryo mammal showing development of diaphragm : Fig. A early stage, Fig. B later stage. A horizontal cut has removed dorsal half and exposed splanchnocoele, etc.; dorsal view. *bd*, Bile duct ; *ca*, coeliac artery ; *cf*, posterior closing fold ; *dc*, ductus Cuvieri passing down into transverse septum ; *dp*, dorsal pancreas ; *fw*, arrow passing through primitive foramen of Winslow ; *i*, intestine ; *lg*, left lung ; *llv*, left lobe of liver ; *luv*, left umbilical vein ; *ms*, median dorsal mesentery ; *nf*, nephric fold (*plpt*, pleuro-peritoneal membrane) ; *phr*, phrenic nerve ; *plp*, pleuro-pericardial membrane ; *plpr*, pleuro-pericardial canal, derived from large opening into pericardial coelom, *pr* ; *pv*, portal vein ; *rpf*, right pulmonary fold ; *rpr*, right pulmonary recess ; *ruv*, right umbilical vein ; *st*, stomach ; *str*, septum transversum ; *vci*, vena cava inferior.

It would be very interesting to know the exact derivation of the muscles of the diaphragm ; unfortunately their origin has not yet been definitely traced. But there can be little doubt that the material from which they develop passes into the transverse septum from the myotomes belonging to the third, fourth, and fifth cervical nerves (which provide the
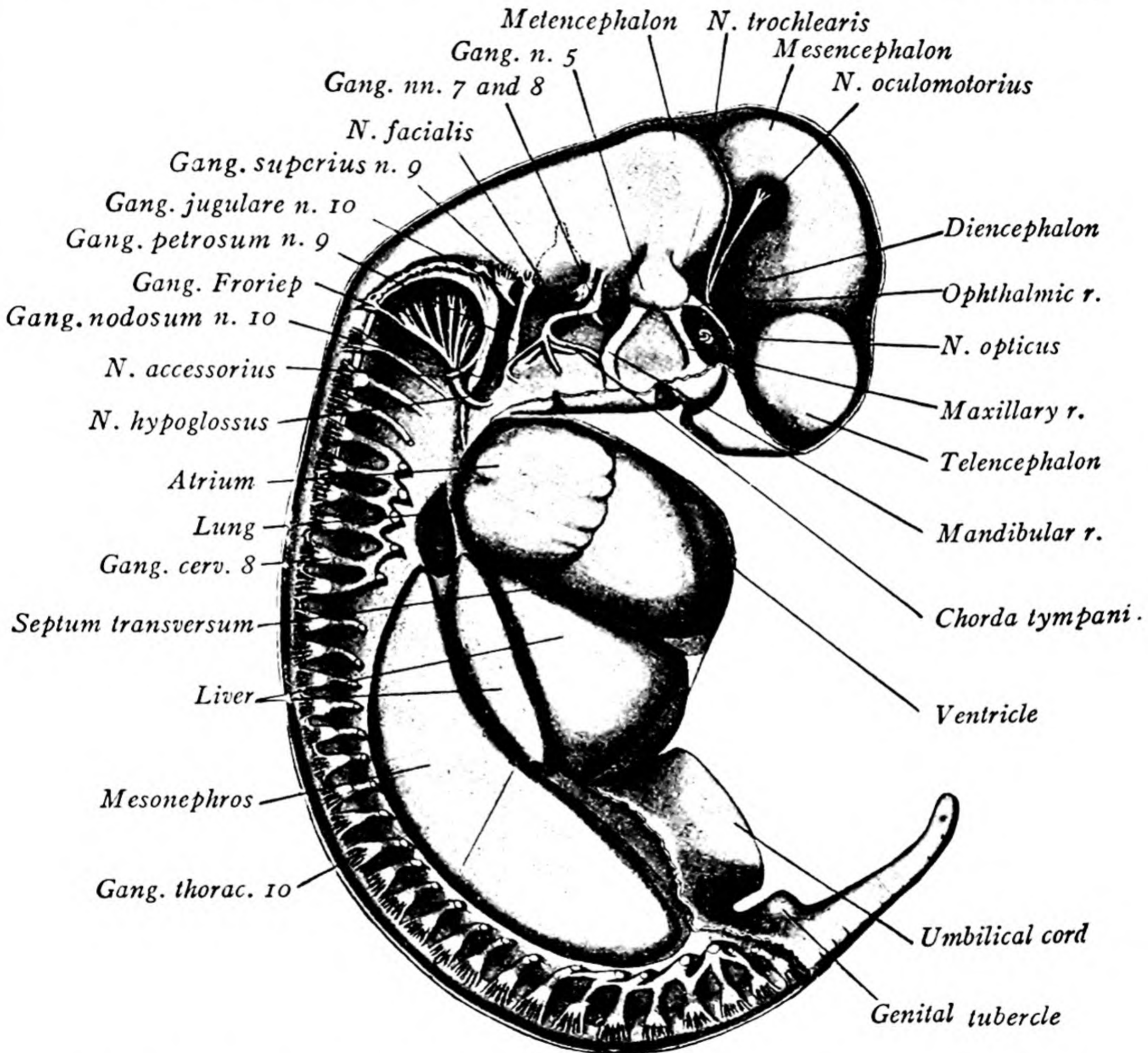
FIG. 651.

Lateral dissection of a 10 mm. pig embryo, showing viscera and nervous system from right side. The eye has been removed and otic vesicle is represented by a broken line. Ventral roots of spinal nerves are not indicated. × 10·5. (From Prentiss and Arey, *Text-book of Embryology*, 1917.) *n*, Nerve ; *r*, ramus.

branches constituting the phrenic nerve of the adult) at an early stage when the septum is still far forward in the future neck region. Bardeen, indeed, has found the rudiment of the diaphragm muscles in the region of the fifth cervical nerve in early human embryos (3).

To sum up the ontogenetic history of the diaphragm. It is of

compound origin ; formed in part ventrally from the transverse septum, dorsally from the pleuro-peritoneal membrane and transverse outgrowths or closing folds from the mesentery on the left and the pulmonary fold on the right. The body-wall itself, when the thorax expands and the
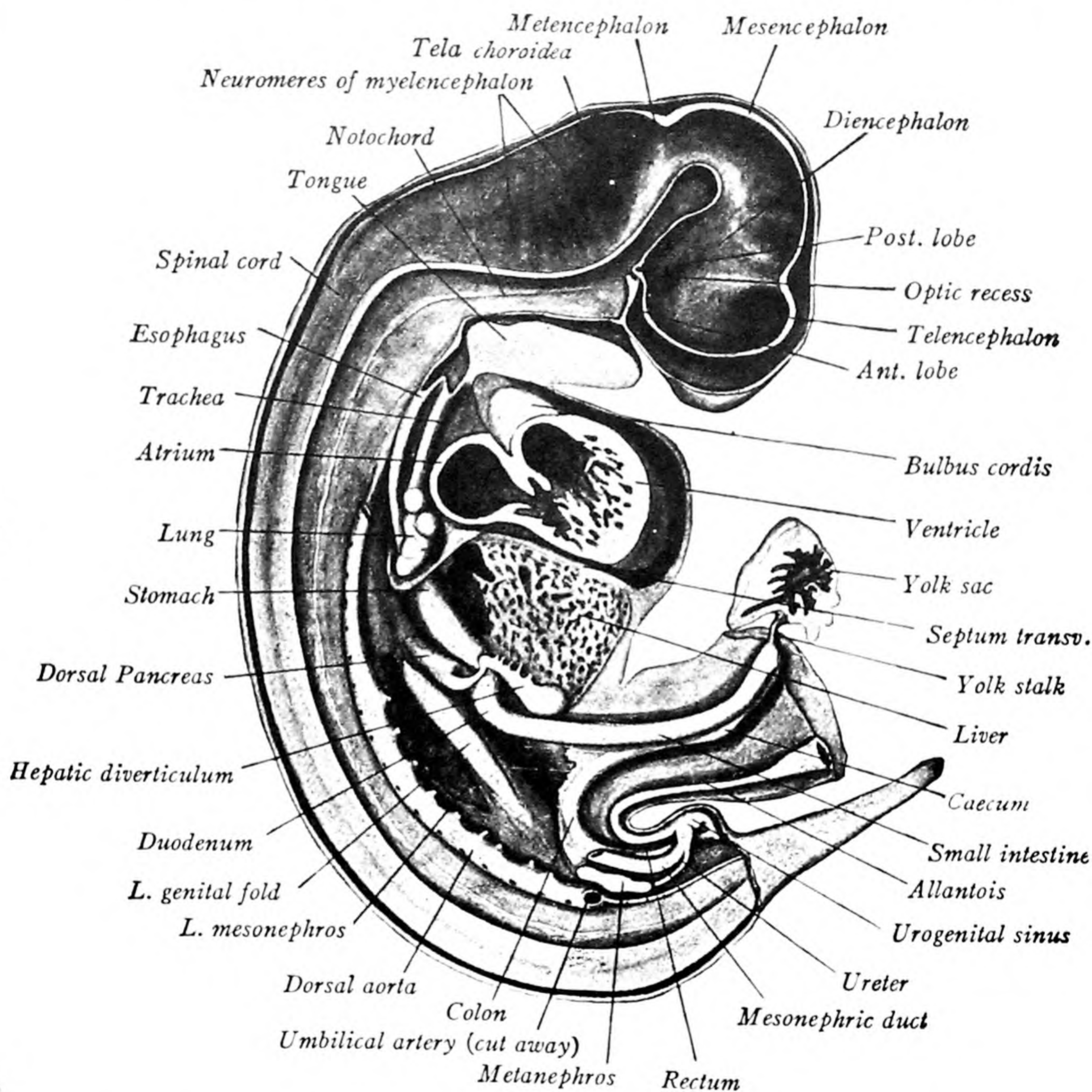
Fig. 652.

Median sagittal dissection of 10 mm. pig embryo, showing brain, spinal cord, and viscera from right side. × 10·5. (From Prentiss and Arey, *Text-book of Embryology*, 1917.)

pleural cavities grow downwards on either side of the pericardium, probably contributes largely to its formation, extending the pleuro-peritoneal membrane and the septum transversum at the sides. In addition to these elements of the diaphragm should also be mentioned the

dorsal and ventral mesenteries, which join the right and left halves, tissue lying on the liver dorsally to the transverse septum, and lastly

Semilunar ganglion n. 5   Ophthalmic ramus n. 5
Gang. geniculi n. 7   Cerebrum
Mesencephalon   Hypophysis
Cerebellum   N. opticus
Gang. acusticum n. 8   Lobus olfactorius
Gang superius n. 9   Maxillary ramus n. 5
Gang. jugulare n. 10   Mand. ramus n. 5
Gang. Froriep   Chorda tympani n. 7
Auricular r. n. 10
Gang. n. cerv. 1
Gang. petrosum n.   N. facialis
N. accessorius
N. hypoglossus   Gang. nodosum n. 10
Gang. cerv. 5–8
Gang. thor. 1
                                          R. atrium
Lung   R. ventricle
Diaphragm   Ventral lobe of liver
Dorsal lobe of liver   Umbilical cord
Mesonephros   Lower limb
Metanephros
Lumbar gang.   Sciatic nerve
Nerve to lower limb

FIG. 653.

Lateral dissection of 35 mm. pig embryo to show nervous system and viscera from right side. × 4. (From Prentiss and Arey, *Text-book of Embryology*, 1917.)

a small contribution from the pulmonary fold (accessory mesentery) on the right of the oesophagus. For it must be remembered that the right

pulmo-hepatic recess in early stages extends forwards into the pleural region in mammals as in other Tetrapods (see p. 631). As the heart moves backwards, the transverse septum shifts from its primitive position far forwards towards the hinder region of the thorax, carrying with it the phrenic nerve and the material from which develop the muscles of the diaphragm.

The history of the complex mammalian diaphragm is doubtless lost with the long line of extinct reptile-like ancestors. Although the elements out of which it has been built, septum transversum, nephric folds, and
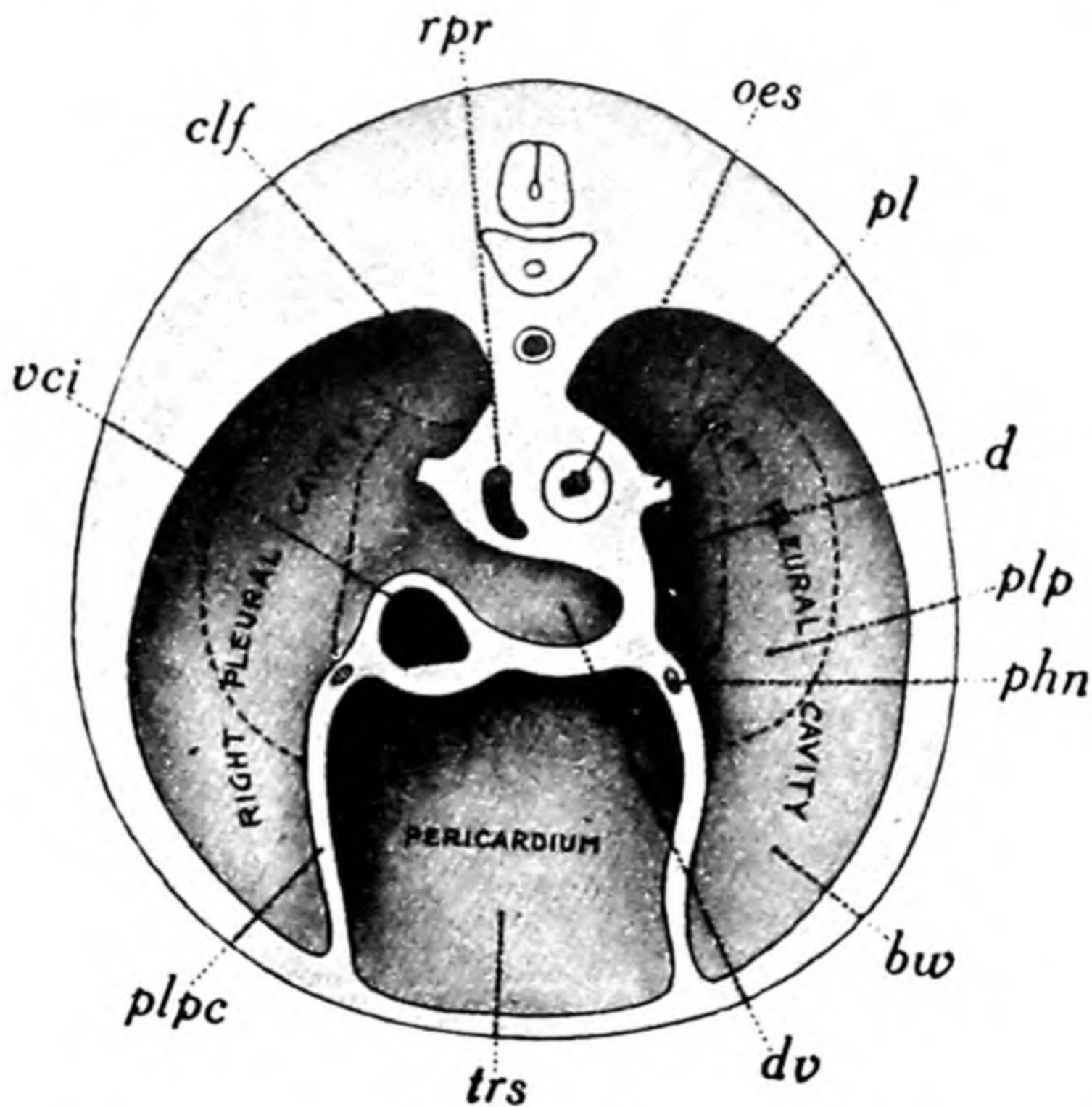
FIG. 654.

Diagram of *diaphragm* of *Mammal*; showing supposed approximate limits (indicated by dotted lines) of various regions derived from different sources. Thorax cut transversely and viewed from in front; heart and lungs removed. Part derived from body wall, *bw*; from posterior closing fold, *clf*; from median mesentery and connective tissue dorsal to liver, *d*; from pleuro-peritoneal membrane, *plp*; from ventral region of transverse septum, *trs*. *dv*, Diverticulum of right pleural cavity; *oes*, oesophagus; *phn*, phrenic nerve; *pl*, cut fold supporting lung; *plpc*, pleuro-pericardial membrane; *rpr*, right pulmonary recess; *vci*, vena cava inferior. (Modified from Broman.)

even posterior closing folds, may all occur in the modern Reptiles, it is not among these that we should expect to find its homologue. Huxley long ago rejected the loose comparisons made by the older authors between the diaphragm of the mammal and the various septa of birds. Indications of the origin of the diaphragm may, however, be sought among Amphibia, though the modern forms are too specialised and too far removed from the mammalian stem to afford much evidence. One of its most character-istic features is its derivation in great part from the septum transversum and the growth into it of somatic muscles supplied from in front by the

phrenic nerve. It seems clear, therefore, that the mammalian diaphragm must have begun to develop as part of the respiratory mechanism when the heart was still far forward, and before the neck region had become differentiated. Now, ever since Breyer (1811) described muscles attached to the base of the lungs in the Surinam toad, *Pipa americana*, anatomists have compared certain muscles found in this region in the Anura with the muscular diaphragm of the mammal (Meckel, 1821; Dugés, 1834; Goette, 1875; Giglio-Tos, 1894, 1906; Beddard, 952; Nussbaum, 1896), and lately the question has been treated in detail by Keith (970). The muscular body-wall of the Amphibia, formed of the rectus abdominis ventrally, splits laterally into external and internal oblique muscles, and again into a superficial external oblique and an internal transversus muscle. While the anterior segment of the rectus abdominis profundus (supplied by the second spinal nerve) becomes attached in Anura Aglossa to the pericardial wall or septum transversum, below and at the sides, the anterior region of the transversus (supplied by the third spinal nerve) is attached to it more dorsally. These two muscles may well represent the material from which the ventral sterno-costal and spinal musculature (similarly supplied from the third, fourth, and fifth spinal nerves, Gössnitz, 966) have been phylogenetically derived. Much the same conditions obtain in the Urodela. Yet the conditions in modern Amphibia differ radically from the mammalian, in that the anterior muscles mentioned above (chiefly the transversus attached to the oesophagus, roots of the lungs, and pericardial wall) serve in them for expiration, and in that inspiration is not brought about by expanding the thorax (see p. 597).

Bertelli (955) denies the possibility of these Amphibian structures having given rise to the muscular diaphragm of the Mammalia. Nevertheless, it seems not impossible that some such extension of muscles into the transverse septum may have taken place in Theromorphous ancestors, and that by the motion backwards of this muscular transverse septum to a position behind the lungs and its combination with the nephric folds, into which the muscles may have penetrated, the mammalian diaphragm may have developed.

CHAPTER XIII

EXCRETORY ORGANS AND GENITAL DUCTS

THE EXCRETORY ORGANS AND GENITAL DUCTS OF CRANIATA

THE kidneys of adult Amniotes are compact organs situated on the roof of the abdominal cavity in the pelvic region. They are covered ventrally by the coelomic epithelium, and consist of a mass of urinary tubules opening into a duct or ureter which runs backwards to open into the cloaca, or its derivative, the urinogenital sinus. The Amphibia have a more extended kidney reaching further forward, and in Pisces and Cyclostomata it may extend almost up to the pericardium. Moreover, while in Amniotes the definitive kidney proper is devoted to the elimination of waste products, and there are separate genital ducts, in lower Gnathostomes the kidney

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and its duct serve also for the passage to the exterior of the spermatozoa. In fact there is reason to believe, as will be explained later (p. 714), that the whole excretory system of the Gnathostomata consisted originally of paired segmental tubules leading by means of a longitudinal duct from the coelom to the exterior, and that, while their original function was to serve as genital ducts in both sexes, their excretory function is secondary and was acquired as the original excretory organs or true nephridia disappeared (p. 718).

To understand the morphology and physiology of the genital and excretory organs of the Craniata it is necessary to study their development
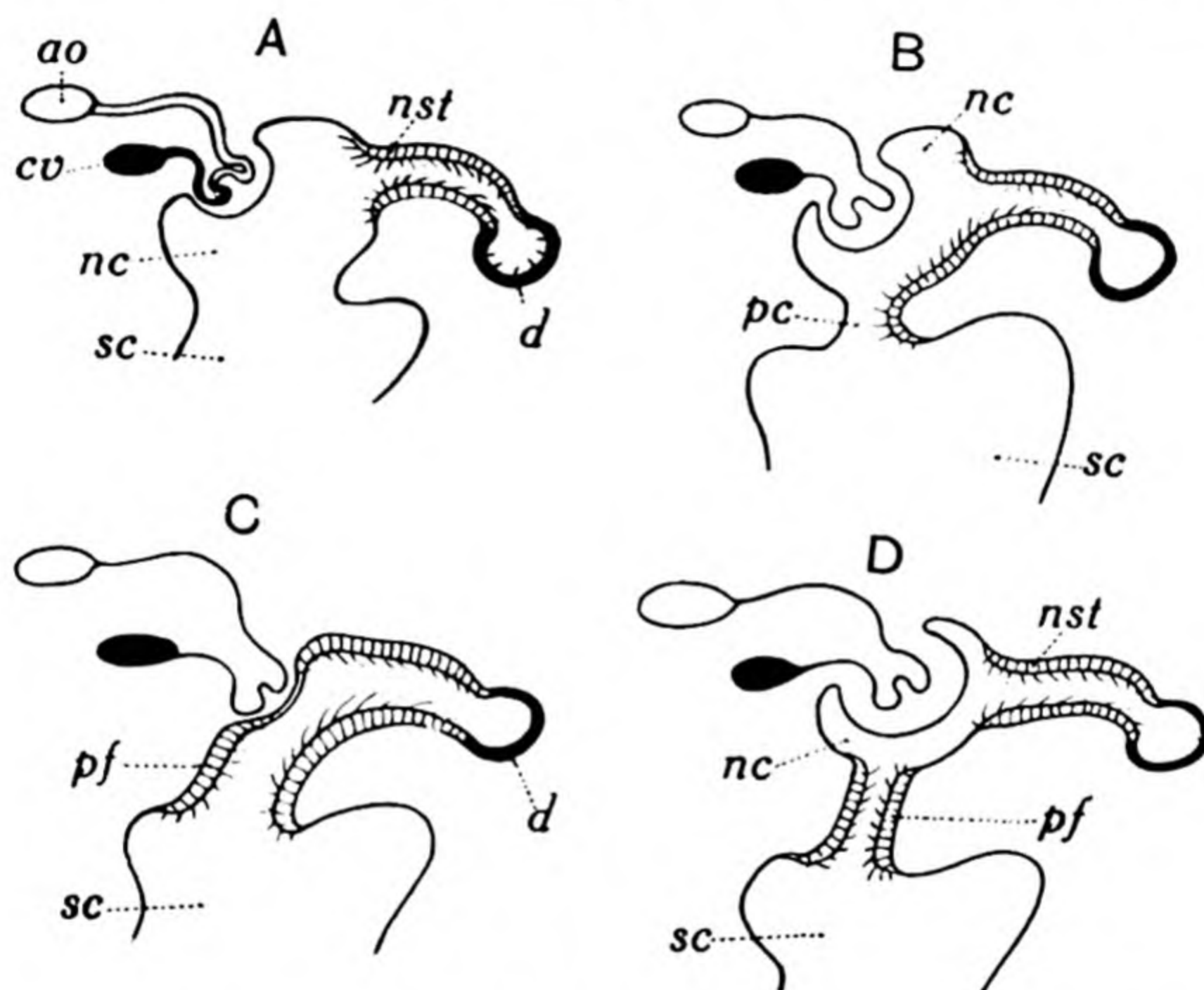
FIG. 655.

Diagrams showing relations of segmental *excretory tubule* of Craniate, and formation of *peritoneal funnel, pf,* and *nephrocoelostome, nst. ao,* Median dorsal aorta supplying artery to glomerulus; *cv,* cardinal vein receiving vein from glomerulus; *d,* transverse section of longitudinal duct; *nc,* nephrocoele; *pc,* communication between latter and general coelom or splanchnocoele.

and modification from Cyclostome to Mammal. But a thorough exposition of the subject would take a volume in itself, and it has been so well dealt with recently in several text-books (Felix, 1005-7; Kerr, 840; Brachet, 993) that it will be sufficient here to give only a general account of some of the more important facts and theories.

The whole excretory system, as it may be called, consists primarily of paired tubules opening on the one hand into the coelom and on the other into a longitudinal duct. The coelomic opening consists of a ciliated 'peritoneal funnel' leading into a narrow 'funnel tubule' which widens out into a thin-walled chamber (Bowman's capsule), one side of which is pushed in by blood-vessels (glomerulus). Capsule and glomerulus

together make up a 'Malpighian body'. From the chamber another ciliated funnel (nephrocoelostome)[1] leads to the coiled 'glandular tubule' which opens into the duct, Fig. 665.

The chief function of the peritoneal funnel seems to be to drive fluid from the coelom towards the tubule, that of the glomerulus to filter fluids from the blood into the cavity of the capsule, and that of the walls of the glandular tubule to excrete nitrogenous waste into its lumen, and to reabsorb some of the fluid. Although the structure just described may be considered as the fundamental plan of the segmental units of the Craniate system, yet such complete tubules are rarely found in the full-grown kidney, owing to the specialisation of some parts and the disappearance of others.
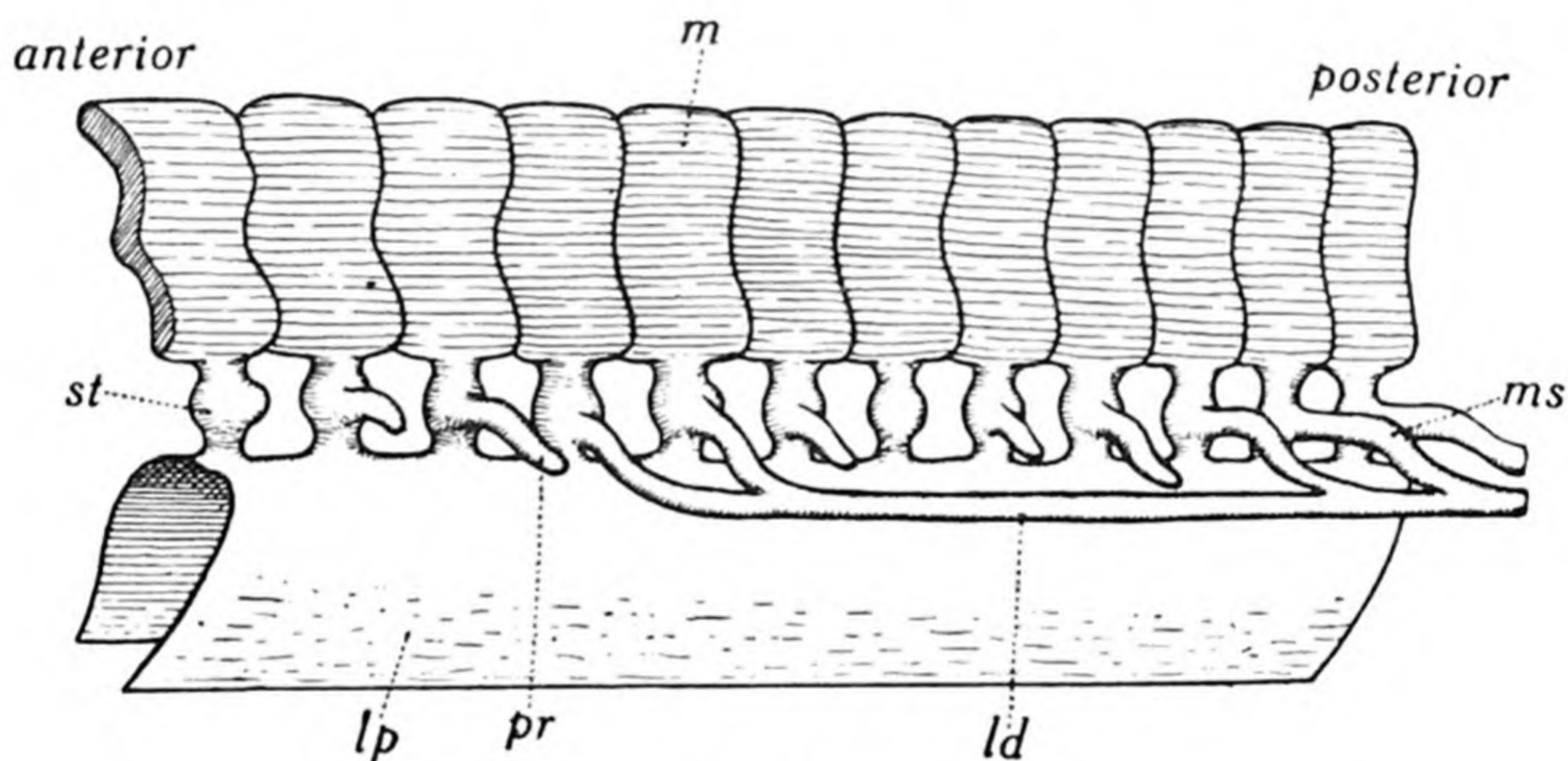
FIG. 656.

Diagram showing development of pronephric, *pr*, and mesonephric, *ms*, tubules from stalk or nephrotome, *st*, joining segmental somites, *m*, to unsegmented lateral plate, *lp*; *ld*, longitudinal duct.

Development.—In accordance with the general differentiation of the segments the tubules develop from before backwards. Usually present at some time in all the trunk segments, they fail to appear in the anterior (head) and posterior segments (tail). There is a tendency for those of the more anterior segments to develop and become functional in early life, and for those of the more posterior segments to develop and function in later life, accompanied by the more or less complete degeneration of the first-formed tubules. While the ancestral Craniate may be supposed to have been provided with a complete set of seg-

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[1] The term 'nephrostome' has been applied to both the peritoneal funnel and the funnel leading from the chamber. The latter is here called nephro-coelostome to emphasise the fact that it is derived from and opens into the nephrocoele (p. 660), and to avoid confusion with the nephrostome of the Annelid nephridium with which it has nothing to do (p. 718).

mental tubules throughout the whole trunk region opening into a longitudinal duct leading to a posterior cloaca, in all existing Craniates a few anterior tubules and their duct develop first, and are later succeeded by a larger number of more posterior tubules opening into the same duct (Cyclostomes, Pisces, Amphibia). Further, in the Amniota, this second set is succeeded by yet more posterior tubules which make up the adult organ. Thus an original complete **archinephros** with its archinephric duct became differentiated into pro-, meso-, and meta-nephros (Lankester's terminology, Fig. 673).
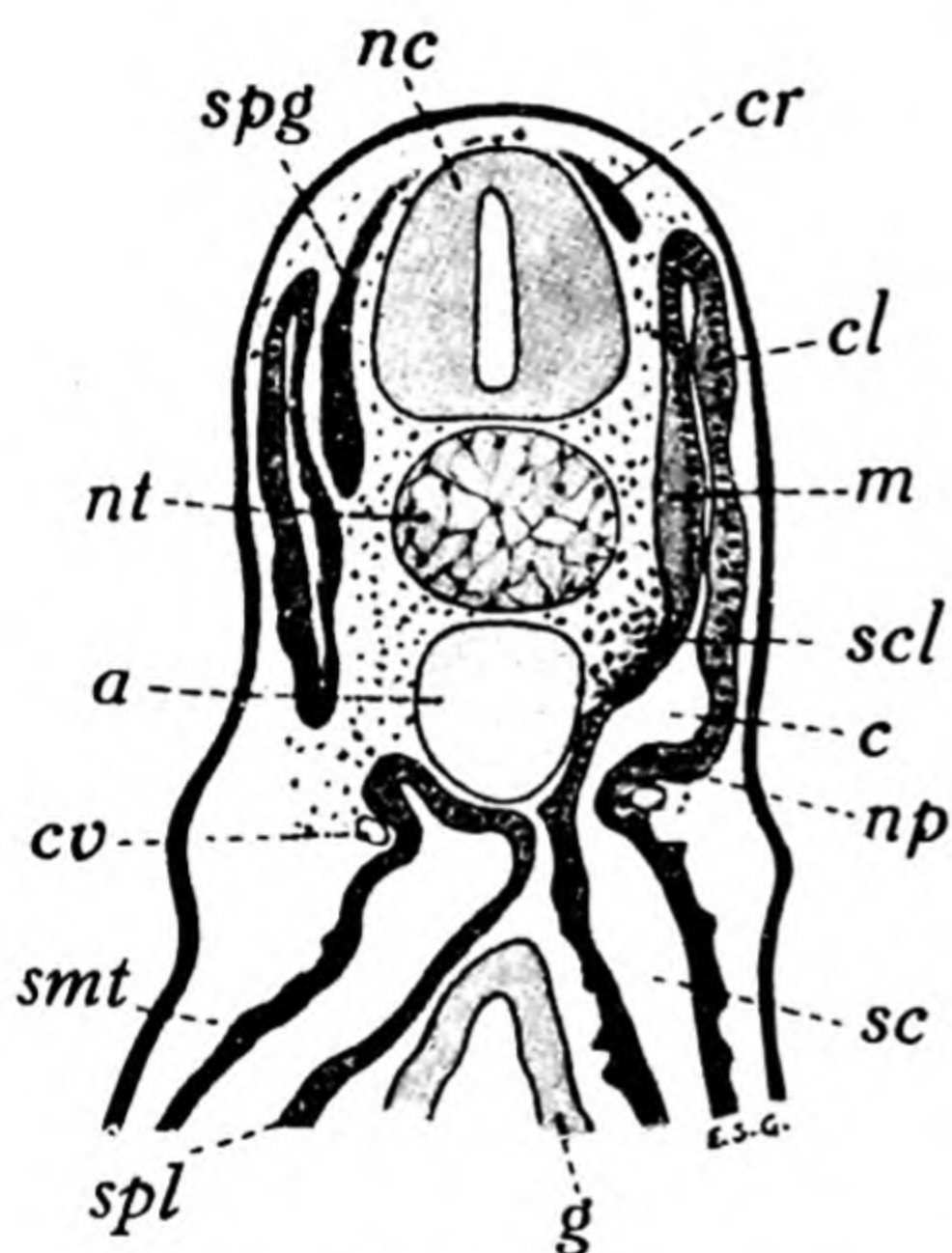
FIG. 657.

Transverse section of *Scyllium canicula*, embryo stage J, taken in front of pronephros. *a*, Dorsal aorta; *c*, nephrocoele; *cl*, outer 'cutis layer' of myotome; *cr*, neural crest; *cv*, cardinal vein; *m*, myomere in inner wall of myotome; *nc*, nerve cord; *np*, rudiment of pronephric nephrocoelostome; *nt*, notochord; *sc*, splanchnocoele; *scl*, sclerotome; *spl*, splanchnopleure; *smt*, somatopleure; *spg*, spinal ganglion; *g*, wall of gut.

It has now been satisfactorily established that all the tubules are developed directly or indirectly from the segmental stalk of mesoblastic tissue which in early stages unites the dorsal segmented somite to the more ventral unsegmented lateral plate (pp. 3, 722). This intermediate region, known as the **nephrotome**, is often hollow from the first or becomes so later, its cavity communicating with the sclero-myocoele above and the splanchnocoele or general coelom below. Soon the nephrotome becomes separated off from the somite and the communication of its cavity (**nephrocoele**) with the sclero-myocoele is cut off, while the opening into the general coelom persists as the peritoneal funnel. Meanwhile from the lateral wall of the nephrotome there grows out a diverticulum towards the ectoderm to form the glandular tubule. The nephrocoele persists as the cavity of Bowman's capsule. In the anterior or pronephric region, at all events, the diverticula (blind at first) lengthen, bend backwards, and fuse at their distal ends to a longitudinal duct, which in the majority of Gnathostomes (Elasmobranchii, Apoda, Amniota) grows back freely between the ectoderm and somatic wall of the coelom to the cloaca. The mesonephric tubules which develop later find the duct ready made, join and open into it. Thus the **primary longitudinal duct** functions at first as a pronephric duct and later as a mesonephric duct behind the pronephric region, Figs. 656, 660, 665.

The development described above becomes variously modified in the different regions and various groups owing to specialisations which often render it difficult to interpret, especially as regards the ducts (see below: Müllerian and Wolffian ducts, etc.).[1]

The pronephric tubules are usually degenerate, incompletely developed, and apparently functionless in Gnathostomes whose embryos are supplied with a large amount of yolk and have no free larval stage (Elasmobranchii, Reptilia, Aves, and in Mammalia), and are fully developed and functional only in those forms with comparatively little yolk and a larval stage (Sedgwick, 1055; Rabl, 1048).

The Pronephros.—Usually far more pronephric rudiments appear than ever reach full development and functional activity, and the best developed remain towards the middle of the pronephric region, the other rudiments at either end of the series soon disappearing. Nor are the rudiments constant in number or in position, although they usually begin only a few segments behind the auditory sac.

Among Gnathostomes a functional pronephros occurs only in Actinopterygii, Dipnoi, and Amphibia. But even in these complete tubules with peritoneal funnel, capsule, and glandular tube are but rarely found (Apoda among Amphibia; Chondrostei, *Amia*, *Lepidosteus* among Actinopterygii). It is, indeed, characteristic of the pronephros that the glandular tube and its nephrocoelostome are usually the only parts typically developed, Figs. 658-68. The nephrocoeles usually expand into thin-walled sacs, and these generally combine on each
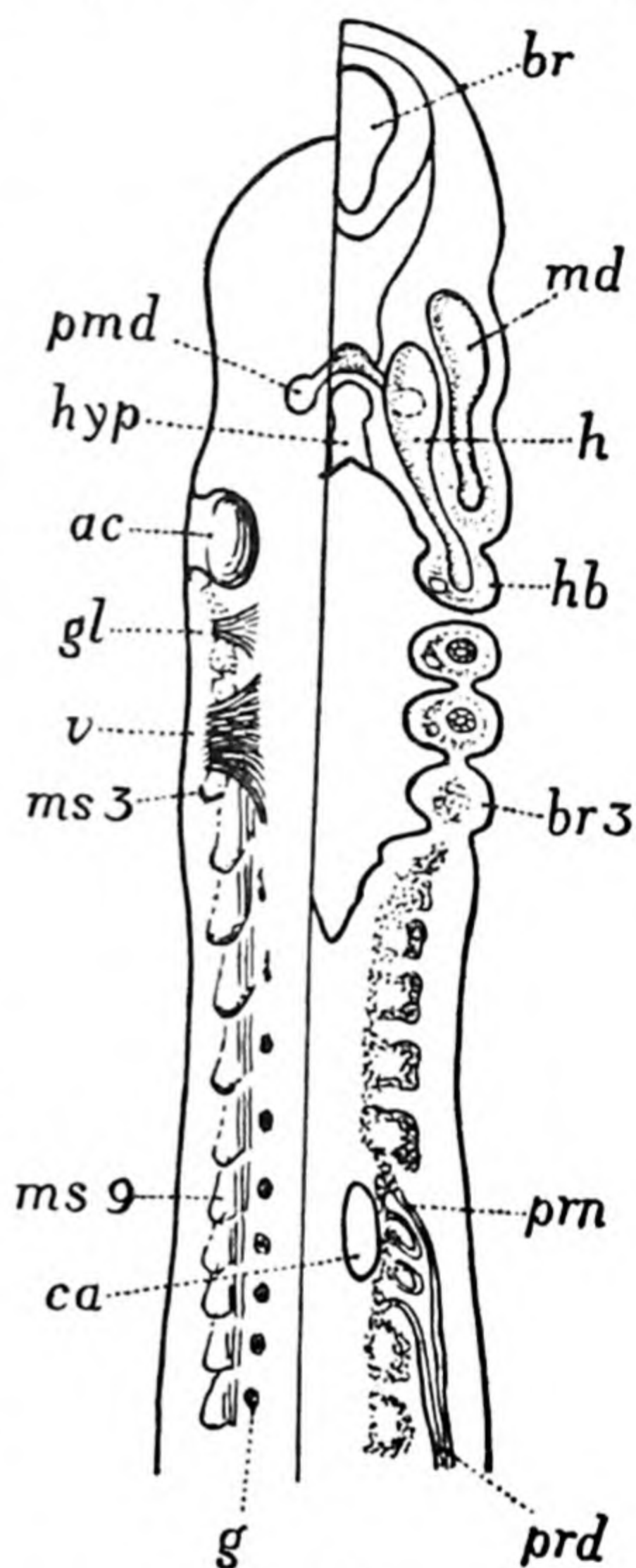
FIG. 658.

Scyllium canicula, embryo stage I. Partial reconstructions of longitudinal horizontal sections, the half on left more dorsal than that on right. *ac,* Auditory sac; *br,* brain; *br* 3, third branchial arch; *ca,* ductus Cuvieri; *g,* spinal ganglion; *gl,* glossopharyngeal nerve; *h,* hyoid somite; *hb,* hyoid bar; *hyp,* hypophysis; *md,* mandibular somite; *ms* 3-9, third to ninth metaotic somites; *pmd,* premandibular somite; *prd,* pronephric duct; *prn,* first of three pronephric funnels (nephro-coelostomes); in front of them are four nephrocoeles.

[1] Further complications are brought about owing to different modes of development of the nephrotome. In many forms (Amphibia and Amniota) it is at first solid, it and the tubule rudiment becoming secondarily hollowed

side to a common pronephric chamber into which open the nephrocoelo-stomes, and project the glomerular vessels joined to a longitudinal vascular ridge or 'glomus'. The corresponding peritoneal funnels disappear as such, the openings becoming widened out and confluent, so that the chamber is more or less completely merged with the general coelom as in Anura. But, as a rule, by the meeting of the two coelomic walls below the chamber it becomes cut off from the more ventral coelom by a floor leaving a wide communication at the posterior or at both ends. In Teleosts the chamber may be completely closed.

In *Polypterus* (Kerr, 1033) about nine nephrocoeles become enlarged, from the first five of which tubules develop, and of these two survive and become functional. Their nephrocoeles fuse to a chamber widely open to the general coelom. The pronephros of the Dipnoi (Semon, 1062 ; Kerr, 840) is similarly developed. In *Lepidosiren* tubule rudiments arise in metaotic segments 5-7 ; two become functional and open into a chamber with a glomus. *Acipenser* (Salensky, 1880–81 ; Jungersen, 1029 ; Maschkowzeff, 1040 ; Fraser, 1011) has some eight rudiments, of which six or seven survive ; in *Lepidosteus* (Balfour, 2 ; Beard, 989 ; Felix, 1005) three, and in *Amia* (Jungersen, 1029 ; Dean, 1002 ; Felix, 1005) three or four survive and become functional out of some eight rudiments, of which the first corresponds to the third myomere. The number of rudiments varies much in Teleosts (Swaen and Brachet, 1066 ; Felix, 1005), beginning at the level of the second myomere in *Leuciscus*, and fourth in *Salmo*. Of the six rudiments in *Salmo* three survive, but in others only one tubule may develop. It is a remarkable fact that the pronephros remains functional in some adult Teleosts (*Fierasfer* and *Zoarces* : Emery, 121 ; *Lepadogaster* : Guitel, 1018).

In the Amphibia there is a well-developed pronephros with generally three coiled tubules in Anura and two in Urodela, which with the coiled anterior end of the duct form a conspicuous organ. The nephrocoelo-stomes open into a chamber with a glomus. But it is especially in the Apoda that the pronephros is large, being in fact better differentiated in this than in any other group of land vertebrates. Rudiments appear

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out. The solid rudiment is known as the 'intermediate cell-mass' (Balfour, 985). It may, as in Teleostei, become separated off very early from the somite, thus seeming to belong to the lateral plate; or it may become early separated from the lateral plate to reacquire its connexion later.

Sometimes, in Amniotes, the pronephric rudiments seem to arise from the unsegmented somatopleure as a continuous ridge which only later becomes subdivided into segmental outgrowths (Burlend in *Chrysemys*, 1000). But this appearance seems to be secondary and related to the late differentiation of the nephrotomes (de Walsche, 1068).

in segments 4-16, and of these the first eight may become fully developed
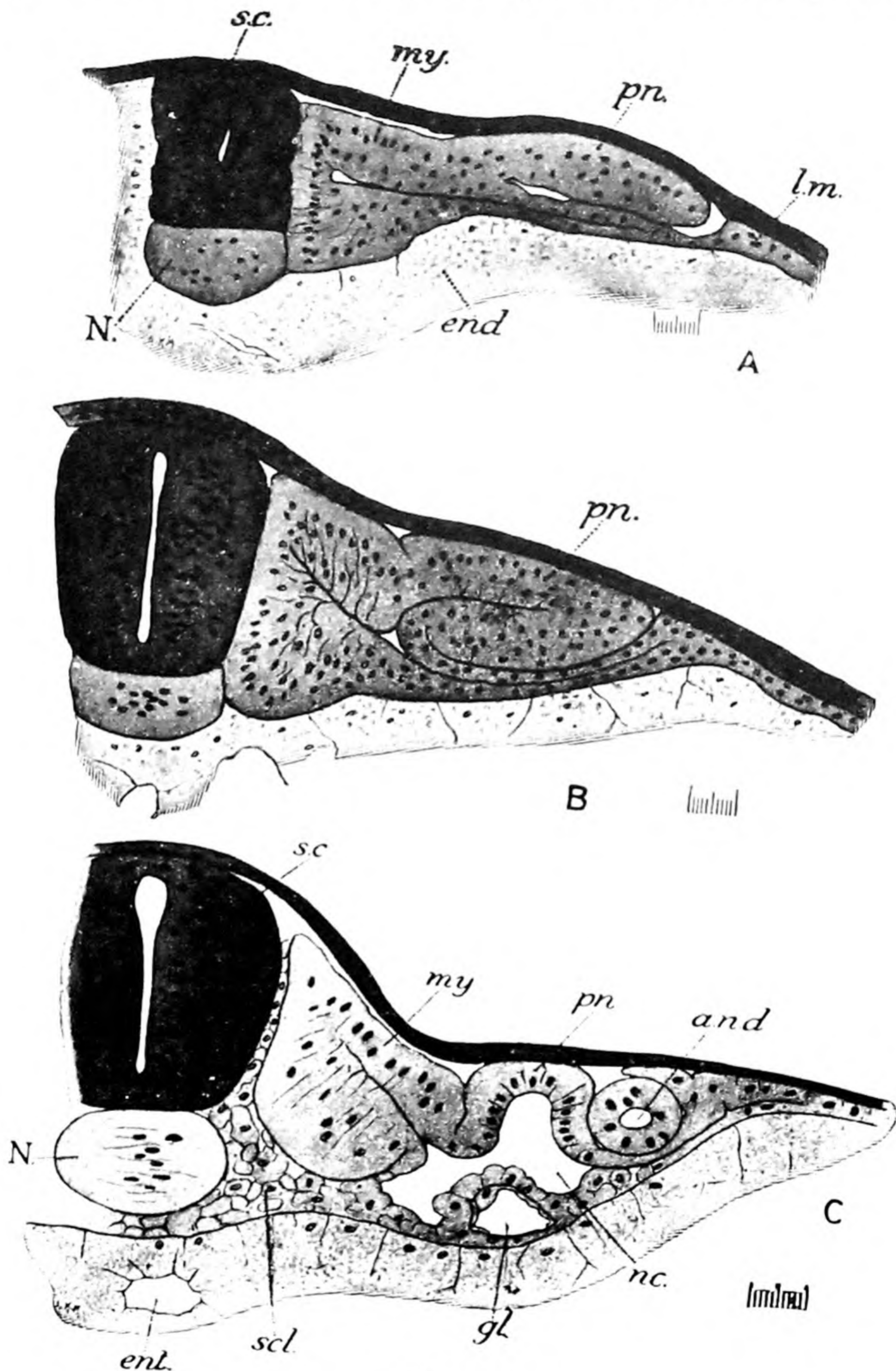
FIG. 659.

Development of the pronephros in *Lepidosiren* as shown in transverse sections. A, Stage 21; B, stage 21; C, stage 24+. *a.n.d*, Archinephric duct; *end*, endoderm; *ent*, enteric cavity; *gl*, glomerulus; *l.m*, lateral mesoderm; *my*, myotome; *N*, notochord; *nc*, nephrocoele; *pn*, pronephric tubule; *s.c*, spinal cord; *scl*, sclerotome. (From Kerr, *Embryology*, 1919.)

and functional (*Hypogeophis*: Brauer, 995). All the parts of a typical

tubule are represented, and the nephrocoeles (Bowman's capsules) remain usually separate, Figs. 665-7.

Although the nephrocoeles of Elasmobranchs may become enlarged in the first 14 trunk segments (v. Wijhe, 1073), only a few produce nephrocoelostomes and tubules (trunk segments 3, 4, and 5 in *Pristiurus*
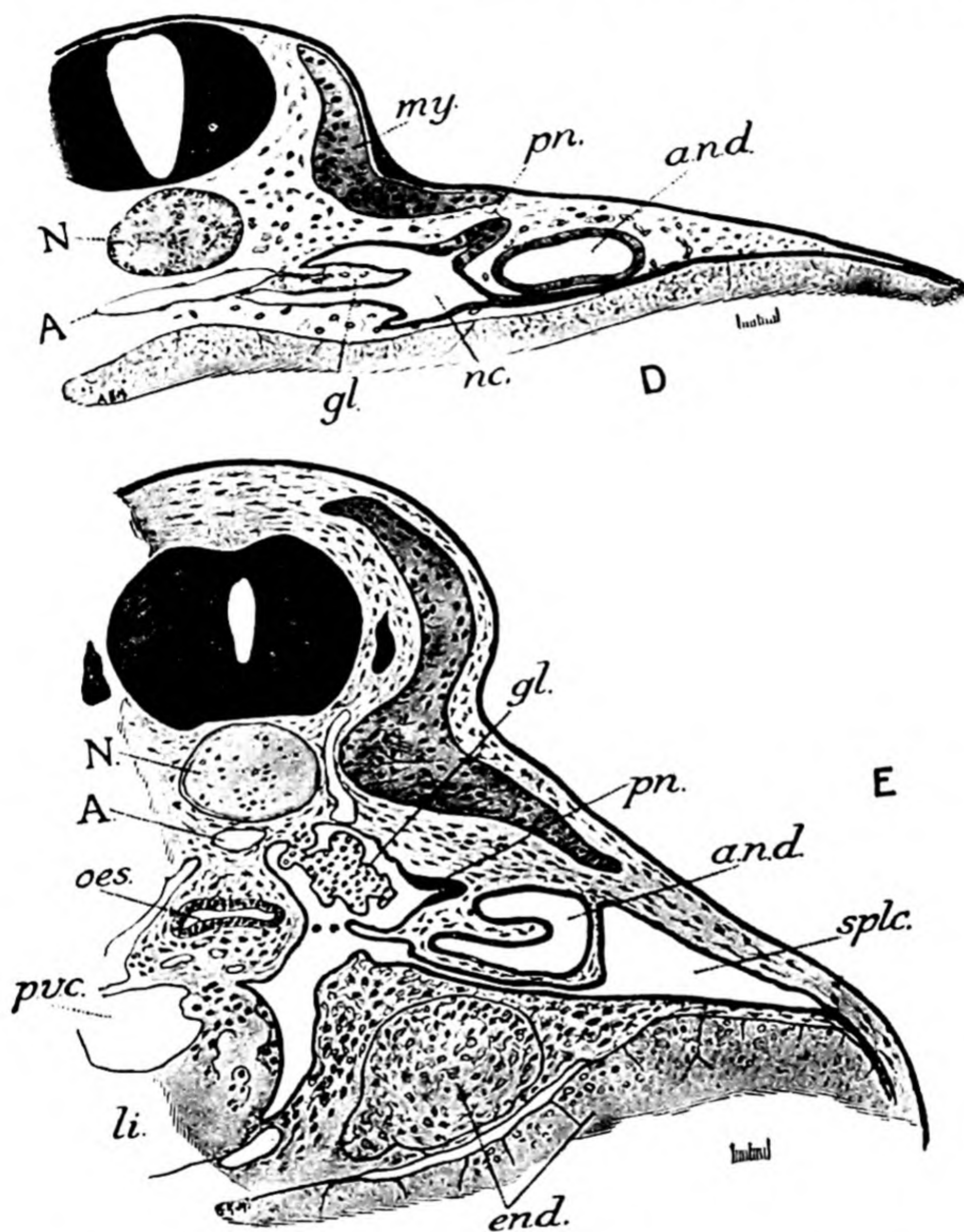
FIG. 660.

Development of the pronephros in *Lepidosiren* as shown in transverse sections. D, Stage 30; E, stage 31+. *A*, Dorsal aorta; *a.n.d*, archinephric duct; *end*, endoderm; *gl*, glomerulus; *li*, liver; *my*, myotome; *N*, notochord; *nc*, nephrocoele; *oes*, oesophagus; *pn*, pronephric tubule; *p.v.c*, posterior vena cava; *splc*, splanchnocoele. (From Kerr, *Embryology*, 1919.)

and *Scyllium*: v. Wijhe; Rabl, 1048—5 tubules in *Raja*: v. Wijhe— 7 in *Torpedo*: Rückert, 1050-51). Neither Bowman's capsules nor glomeruli are formed, although blood-vessels pass down between the successive tubules from the aorta to the wall of the gut where they join the subintestinal vein, Figs. 658, 661 (Mayer, 850; Rabl, 1048; Rückert, 1050).

In Reptiles the pronephros is usually vestigial, but in Chelonians and Crocodilians it is functional for a time (Wiedersheim, 1890; de Walsche, 1068); large nephrocoeles appear in many anterior segments (from about the fourth to thirteenth metaotic segment in *Lacerta*: Hoffmann, 1022; Kerens, 1031). Only the last five to seven of these nephrocoeles in Lizards and Snakes produce tubules, and neither glomeruli nor capsules are formed (Milhalkovics, 1041; Strahl, 1882; Schreiner, 1053; Kerens, 1031).

The very similar pronephros of Birds stretches over some twelve segments beginning about the third metaotic, Fig. 668 (Sedgwick, 1055; Renson, 1883; Schreiner, 1053; Felix, 1005; Keibel and Abraham, 1900; Soulié, 1902; Kerens, 1031).

The mammalian pronephros, seen by earlier observers, but first clearly identified as such by Rabl, 1896, extends over about eight segments from probably the sixth metaotic; but is still more vestigial than in lower Amniotes, the tubules soon fusing to a solid rod or 'pronephric ridge' (Martin, 1039; Bonnet, 1887-8; Kerens, 1031; Fraser, 1010).

The Primary or Pronephric Duct.—As already mentioned, the anterior end of the primary or pronephric duct (segmental duct, primärer Harnleiter) is derived from the fusion of the outer ends of the pronephric tubules. The solid rod of cells so formed grows back-

FIG. 661.

Horizontal section through rudiment of right pronephros of *Torpedo*. (After Rückert, 1888.) *a.n.d*, Archinephric duct; *b.v*, blood-vessel; *pn.1*, etc., pronephric tubules. The nephrotomes are numbered with Roman numerals. (From Kerr, *Embryology*, 1919.)

wards in most Gnathostomes between the ectoderm and the somatic wall of the coelom, becomes hollowed out to a tube, fuses with the wall of the cloaca, and finally opens into its cavity, Figs. 656, 658-9, 664. The prolonged controversy as to whether the growing tip of the duct receives cells from the ectoderm to which it is often very closely applied (v. Wijhe, 1073; Beard, 988; Rückert, 1050; Laguesse, 1891; and others) has been set at rest, and it is now generally admitted that the duct is of purely mesodermal origin (Rabl, 1048; Field, 1008; Felix, 1005; Gregory, 1897; and others). Nevertheless, its exact mode of origin in many forms is still a matter of dispute; for, although its free growth backwards has been shown to occur in

FIG. 662.

Renal organs of the right side of a *Protopterus* larva of stage 34. (From a reconstruction by M. Robertson.) *a.n.d* Archinephric duct; *op*, opisthonephric tubules; *pn*, pronephros. The capital letters indicate funnels and the figures metotic* mesoderm segments. (From Kerr, *Embryology*, 1919.)

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* 'Metotic' = posterior to the otocyst.

Elasmobranchs (Balfour, **985**; Rabl, **1048**; Bates, **987**), Apoda (*Hypogeophis*, Brauer, **995**), and Amniotes (Weldon, **1071**, Hoffmann, **1022**, in Reptiles; Sedgwick, **1055-6**, Schreiner, **1053**, Felix, **1005**, in Birds; Martin, **1039**, in Mammals; Kerens, **1031**, in Amniota), yet in other groups it appears to develop differently.

In Urodela and Anura, according to Mollier (**1043**) and Field (**1008**), it develops as a longitudinal thickening and folding off of the mesoderm of the nephrotomal region and only grows out freely at the extreme posterior end to join the cloaca. Much the same mode of development is described in Teleosts (Swaen and Brachet, **1066**; Felix, **1005**) and other Actinopterygii (*Acipenser*, Maschkowzeff, **1040**; Fraser, **1011**; *Polypterus*, Kerr, **1033**). The morphology of the pronephric duct is further discussed below (p. 684).

The Mesonephros and its Duct.—The mesonephric tubules of Gnathostomes appear later than the pronephric, arising from more posterior nephrotomes. At first they are strictly segmental. In Pisces, Amphibia, and Reptilia peritoneal funnel, Bowman's capsule, glomerulus, and glandular tube are usually typically developed throughout the series, excepting for the first and last few rudiments which may be vestigial, Figs. 656, 673-4. (Transitory vestigial closed peritoneal funnels appear as a rule in Birds and Mammals, but open tubes are only fully developed in connexion with the testis, p. 686.) The growing outer tip of the tubule fuses with and opens into the ready-formed pronephric duct, which therefore becomes in this region the

mesonephric (Wolffian) duct, and is known by this name. The position of the first-formed tubule varies in different forms, but appears usually
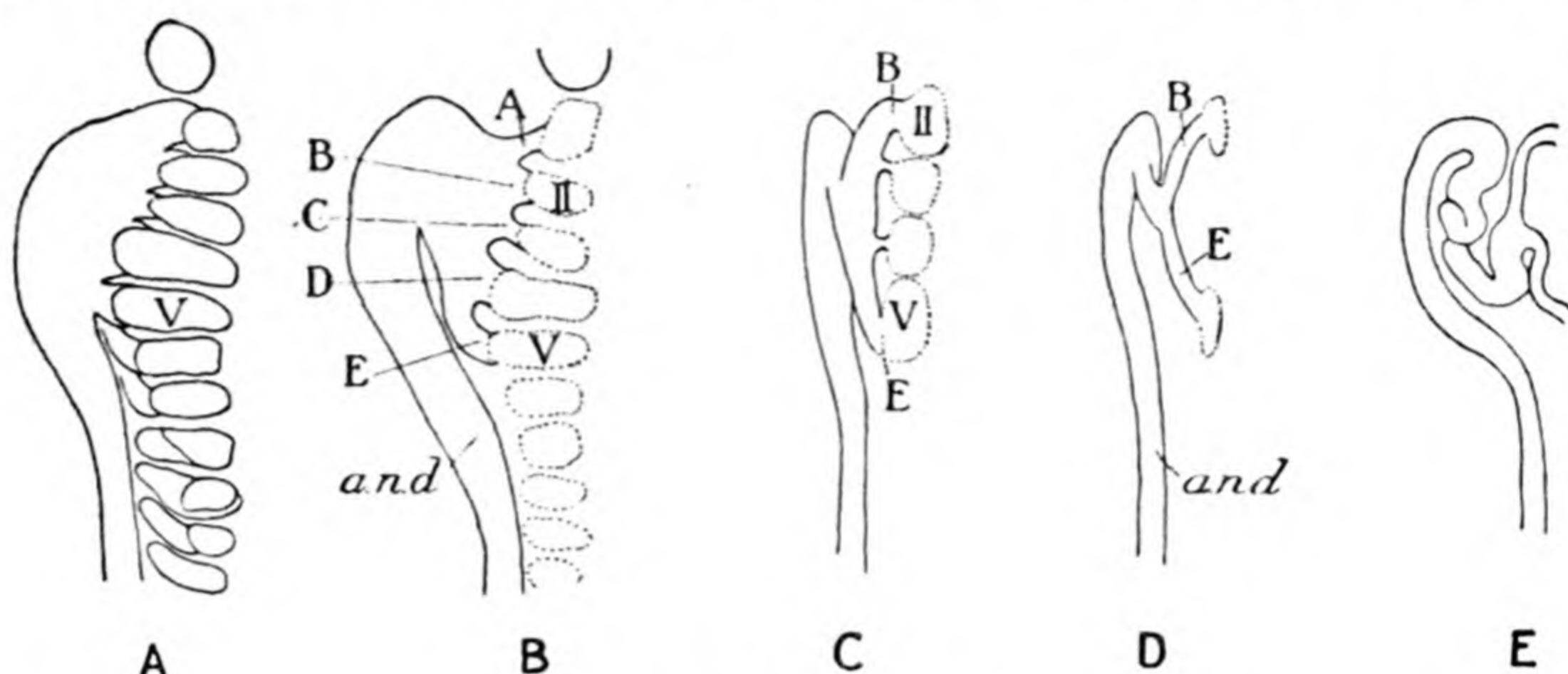
FIG. 663.

Dorsal view of pronephros of *Polypterus* at stages 20, 23, 24+, 25, and *about* 28. *a.n.d*, Archinephric duct. The tubule rudiments are indicated by letters, the nephrotomes by Roman numerals. (From Kerr, *Embryology*, 1919.)

close behind the last pronephric rudiment. It may belong to the next segment ; or there may be a gap between pronephros and mesonephros, which tends to widen with age owing to the disappearance of evanescent tubule rudiments (generally of about 8 segments in Selachii, 3 in *Acipenser*, 16 in *Amia*, 2-17 in Amphibia).

Many observers have helped to work out the history of the mesonephros, among whom may be mentioned : Balfour (985), Sedgwick (1056), v. Wijhe (1073), Rückert (1050-51), Rabl (1048), Borcéa (991), in Elasmobranchs ; Balfour and Parker (2), Beard (1889), in *Lepidosteus* ; Salensky (1880-81), Jungersen (1029), Maschkowzeff (1040), in *Acipenser*; Jungersen (1029), Dean (1002), Felix (1005), in *Amia* ; Semon (1062), Kerr (840), in Dipnoi ; Budgett

FIG. 664.

Transverse section through *Polypterus* of stage 23 at level of cloacal opening. *a.n.d*, Opening of archinephric duct into cloaca ; *cl.* opening of cloaca to exterior ; *end*, alimentary canal rudiment ; *my*, myotome; *N*, notochord; *s.c*, spinal cord. (From Kerr, *Embryology*, 1919.)

(10), Kerr (1033), in *Polypterus* ; Felix (1005), Audigé (982), Guitel (1018), in Teleosts ; Fürbringer (1012), Field (1008), Brauer (995), in Amphibia ;

Hoffmann (1022), Sedgwick (1056), v. Milhalkovics (1041), Schreiner (1053), Gasser (1872–84), Gregory (1900), Abraham (1901), Fraser (1010), in Amniotes.

It is characteristic of the mesonephros of Gnathostomes that its primitive early segmentation is always lost owing to the development of secondary tubules, many of which may appear in each segment. These tubules are derived from embryonic tissue of the nephrotome, remaining after the production of the first series, and usually proliferating from near Bowman's capsule. Several successive generations of tubules may be
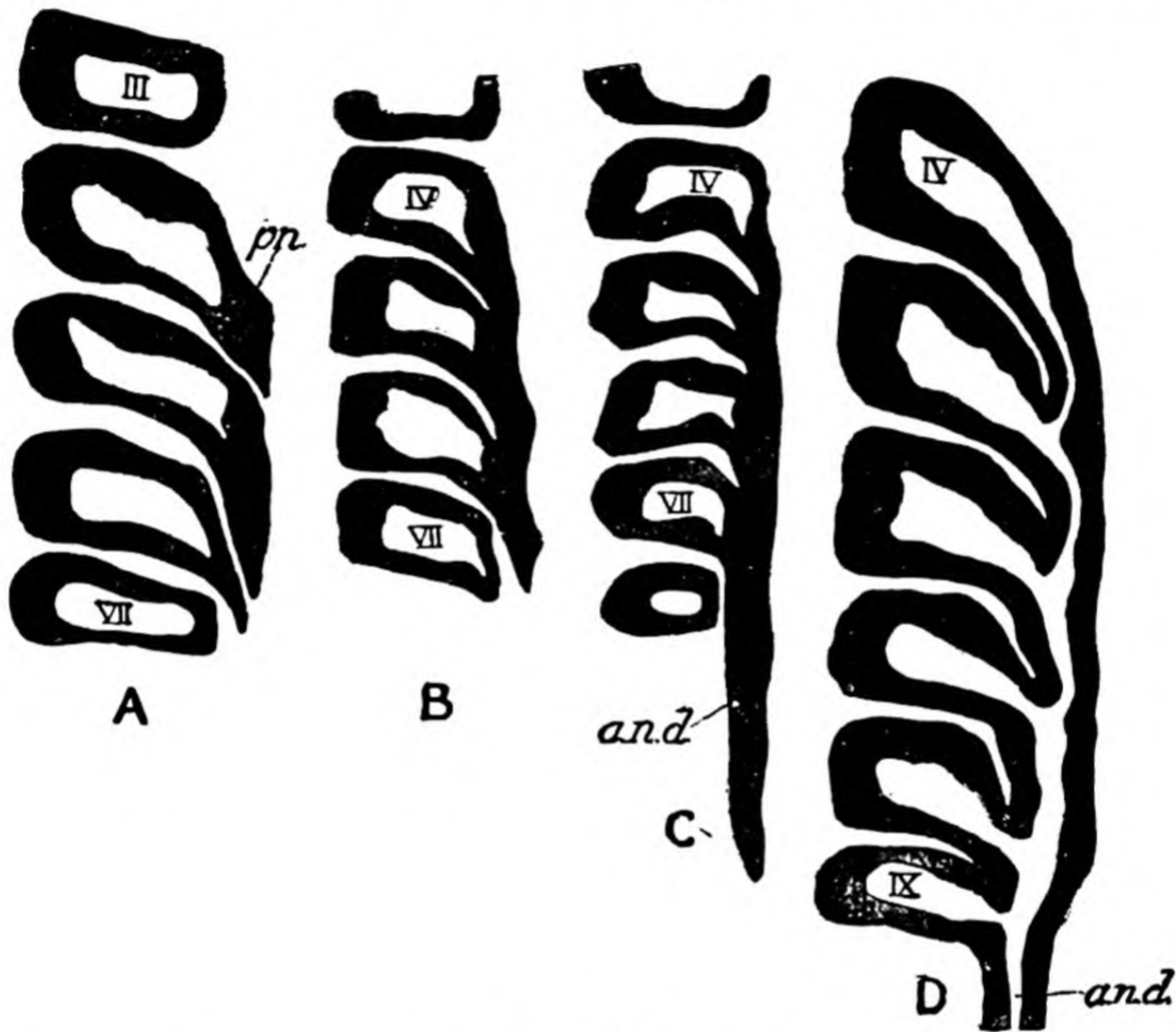
FIG. 665.

Early stages in the development of the pronephros of *Hypogeophis*. Each figure represents a longitudinal section, so arranged as to pass outwards through the nephrotomes, cutting them across, and viewed from the dorsal side. (After Brauer, 1902, slightly simplified.) A, From an embryo with 15 mesoderm segments; B, 12 segments; C, 16 segments; D, 27 segments. *a.n.d*, Archinephric duct; *pn*, pronephric tubule. The Roman figures are placed in the nephrocoeles. (From Kerr, *Embryology*, 1919.)

added from this tissue, each one more dorsal than the last formed. As a rule they develop only a capsule, glomerulus, and glandular tube, but do not acquire a peritoneal funnel. They come to open at the base of the primary tubule leading to the longitudinal duct. According to Borcéa (991) a portion of the collecting tubule or region next to the duct is derived from an outgrowth of the wall of the latter in Selachii, Figs. 669–75.

Except when they convey the spermatozoa from the testis in the male (p. 686), the peritoneal funnels are usually closed in the adult. In many

Selachii, however, in *Amia*, and in Amphibia, they remain open to the
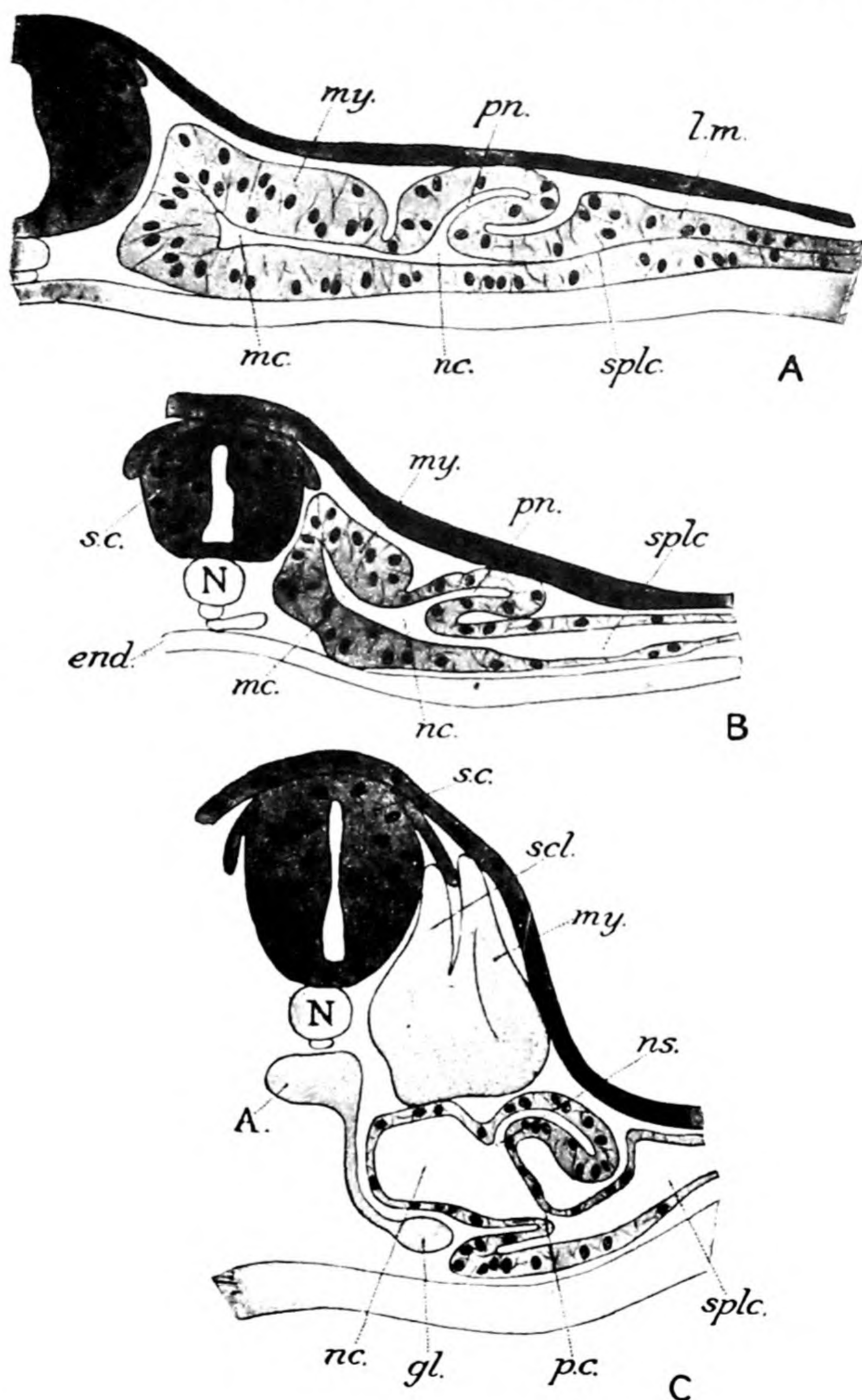
FIG. 666.

Development of pronephros of *Hypogeophis* as seen in transverse sections. (After Brauer, 1902.) A, Embryo with 22 segments; B, with 29 segments; C, with 44 segments. A, Dorsal aorta; *end*, endoderm; *gl*, glomerulus; *l.m*, lateral mesoderm; *mc*, myocoele; *my*, myotome; *N*, notochord; *nc*, nephrocoele; *ns*, nephrocoelostome; *p.c*, peritoneal canal; *pn*, pronephric tubule; *s.c*, spinal cord; *scl*, sclerotome; *splc*, splanchnocoele. (From Kerr, *Embryology*, 1919.)

coelom; but their connexion with Bowman's capsule is often lost (Selachii: Borcéa, **991**), and in Anura (Spengel, **1064**; Nussbaum, **1045**) they come to

open secondarily into the veins, Fig. 671 (cf. pronephros of Myxinoids, p. 676).

Characteristic of the mesonephros of the lower Gnathostomes is the tendency of its more anterior region to become reduced, acquire but few secondary tubules, and even degenerate more or less completely. In the Amniota, of course, it disappears (excepting for its duct and the tubules leading from the testis and corresponding vestiges in the female) completely as a functional excretory organ in embryonic or very early adult
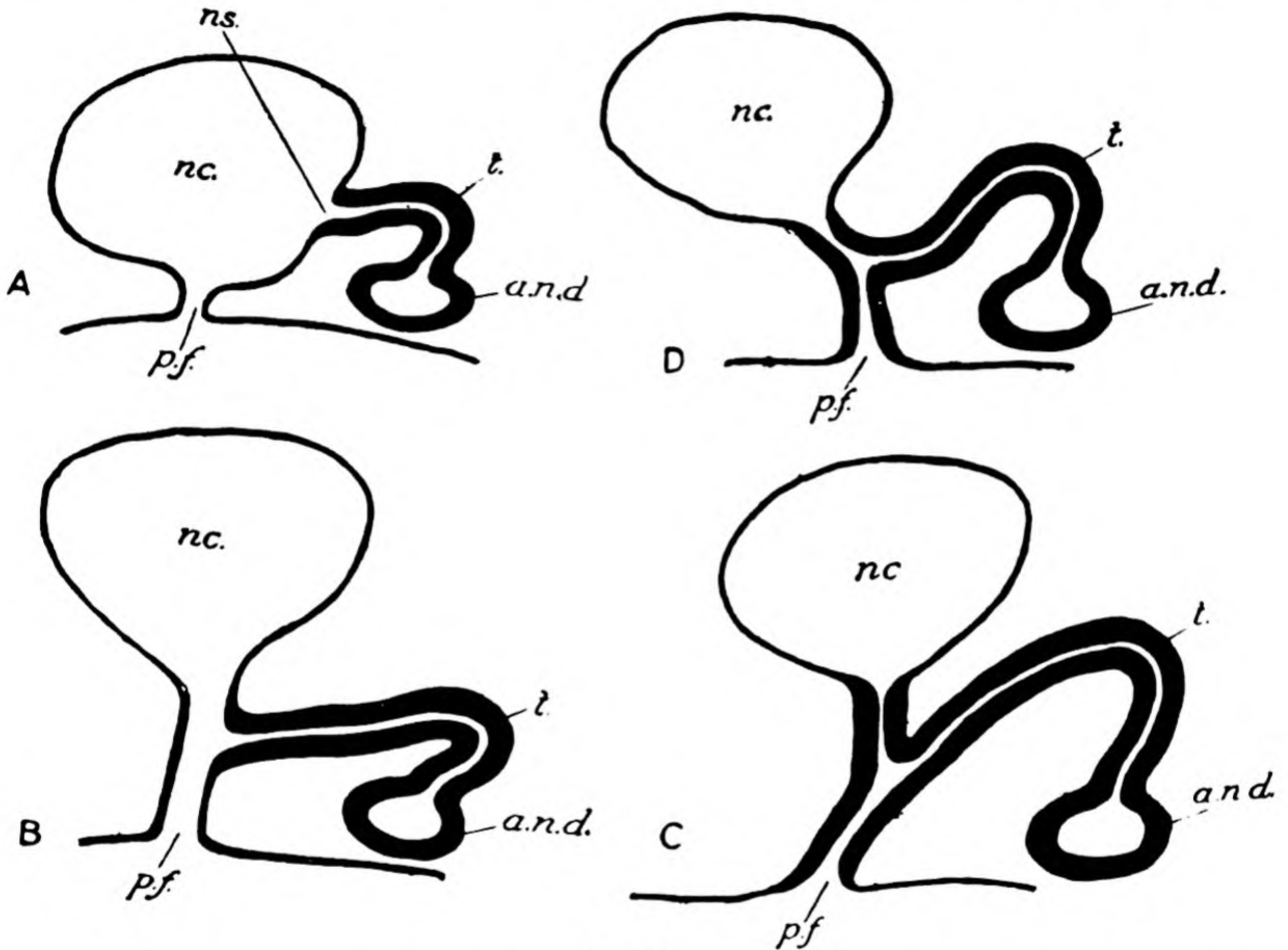
FIG. 667.

Illustrating variations in the relations of nephrocoele, tubule, and peritoneal canal in the pronephros of *Hypogeophis*.　*a.n.d*, Archinephric duct ;, *nc*, nephrocoele ; *ns*, nephrocoelostome ; *p.f*, peritoneal funnel ; *t*, tubule. (From Kerr, *Embryology*, 1919.)

life ; but even in Amphibia and Pisces the more posterior tubules tend to take on the chief excretory function and form the bulk of the adult organ, the hinder part of which may be developed from segments behind the cloaca (caudal kidney of Elasmobranchs and Teleosts). There is a general tendency for the openings of the tubules into the duct to shift backwards and even to combine, and these tubules may form a special duct opening at the base of the mesonephric duct (Selachii, Teleostei), and acquire a special blood supply from the aorta not belonging to the renal portal system. So marked is the tendency towards the differentia-

tion of a special posterior kidney that this region has sometimes been called a metanephros. It is better, however, to reserve the name metanephros for the kidney of the adult Amniote with its special characteristics. Kerr has suggested the term ' opisthonephros ' to include the whole series of tubules behind the pronephros in the lower Gnathostomes where a true metanephros is not present, Fig. 684.

The tubules of the anterior region of the mesonephros in Pisces tend to degenerate and become converted into a ' lymphoid ' organ. This is most conspicuous in the Teleostei, where a large anterior mass is formed, composed chiefly of a network of blood-vessels, lymphatic bodies, and suprarenal elements (Audigé, 982).

The Metanephros and its Duct.—The definitive excretory organ of the Amniota may be defined as the true metanephros. This kidney takes on
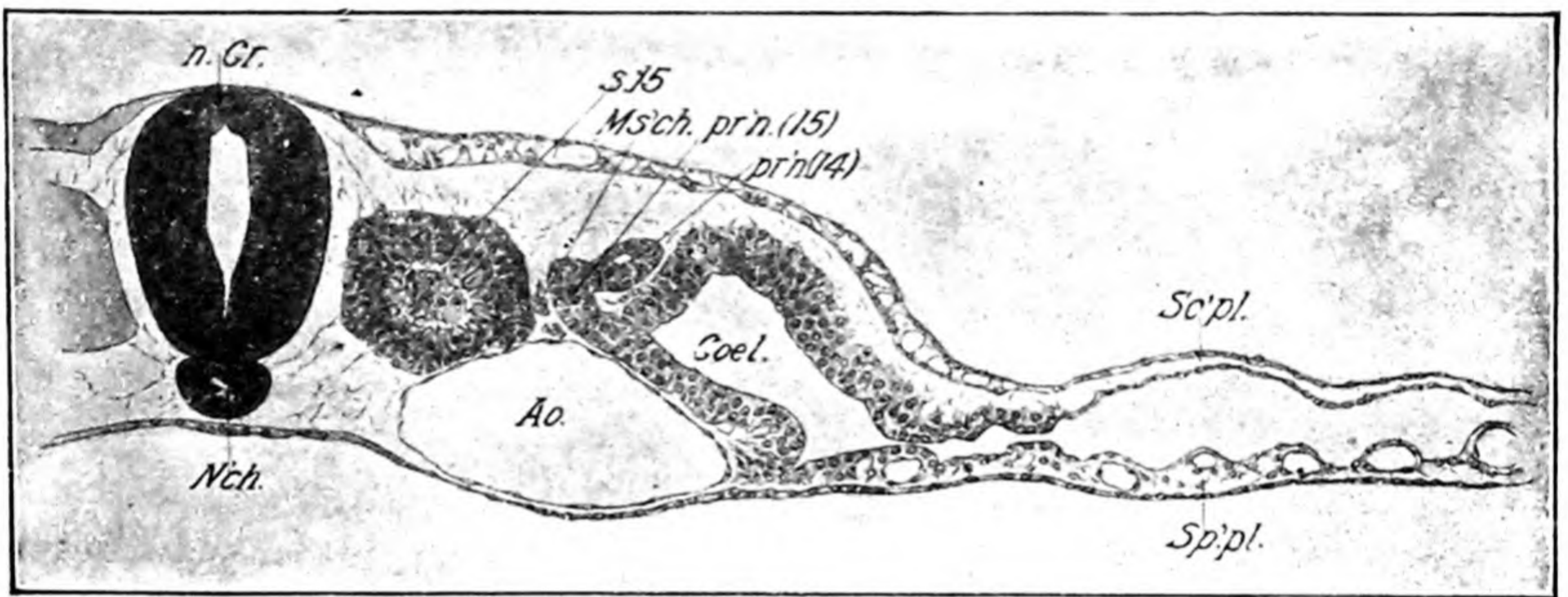
FIG. 668.

Transverse section through the fifteenth somite of a 16 s. embryo (from F. R. Lillie, *Develt. Chick*, 1919). *Ao*, Aorta; *Coel*, coelom; *Nch*, notochord; *Ms'ch*, mesenchyne; *n.Cr*, neural crest; *pr'n* (14), (15), pronephric tubules of the fourteenth and fifteenth somites; *S.15*, fifteenth somite; *So'pl*, somatopleure; *Sp'pl*, splanchnopleure.

the excretory function in Reptiles, Birds, and Mammals, as the mesonephros degenerates; it has no connexion with the gonads. Developing relatively late, when the differentiation of other tissues is far advanced, it is found to arise from paired bands of ' nephrogenous tissue ' following immediately behind that which gave rise to the mesonephros and like it originally derived from nephrotomes. These have long since separated off from their somites, practically all trace of segmentation is lost, and it is not possible to say how many segments may have contributed to the metanephrogenous mass—probably few and possibly only one. The ureter first appears as a diverticulum of the base of the mesonephric duct; it grows forwards and dorsally into the metanephrogenous tissue and with it extends dorsally to the mesonephros, Fig. 676. From the blind end of the ureter grow out numerous slender diverticula round which the nephrogenous tissue becomes grouped. From the latter develop a multitude

of tubules each with a Bowman's capsule into which penetrates a glomerulus, and a coiled glandular section; these open into the diverticula which become the collecting tubules leading to a central expansion of the ureter, the pelvis of the kidney. Since all the tubules are of a secondary nature, no peritoneal funnels occur. The ureter comes to open separately later into the cloaca when the base of the mesonephric duct is merged into its wall, Figs. 677, 699-705.

It is clear that the metanephros does not differ in important essentials either in structure or in development from the mesonephros. Indeed,
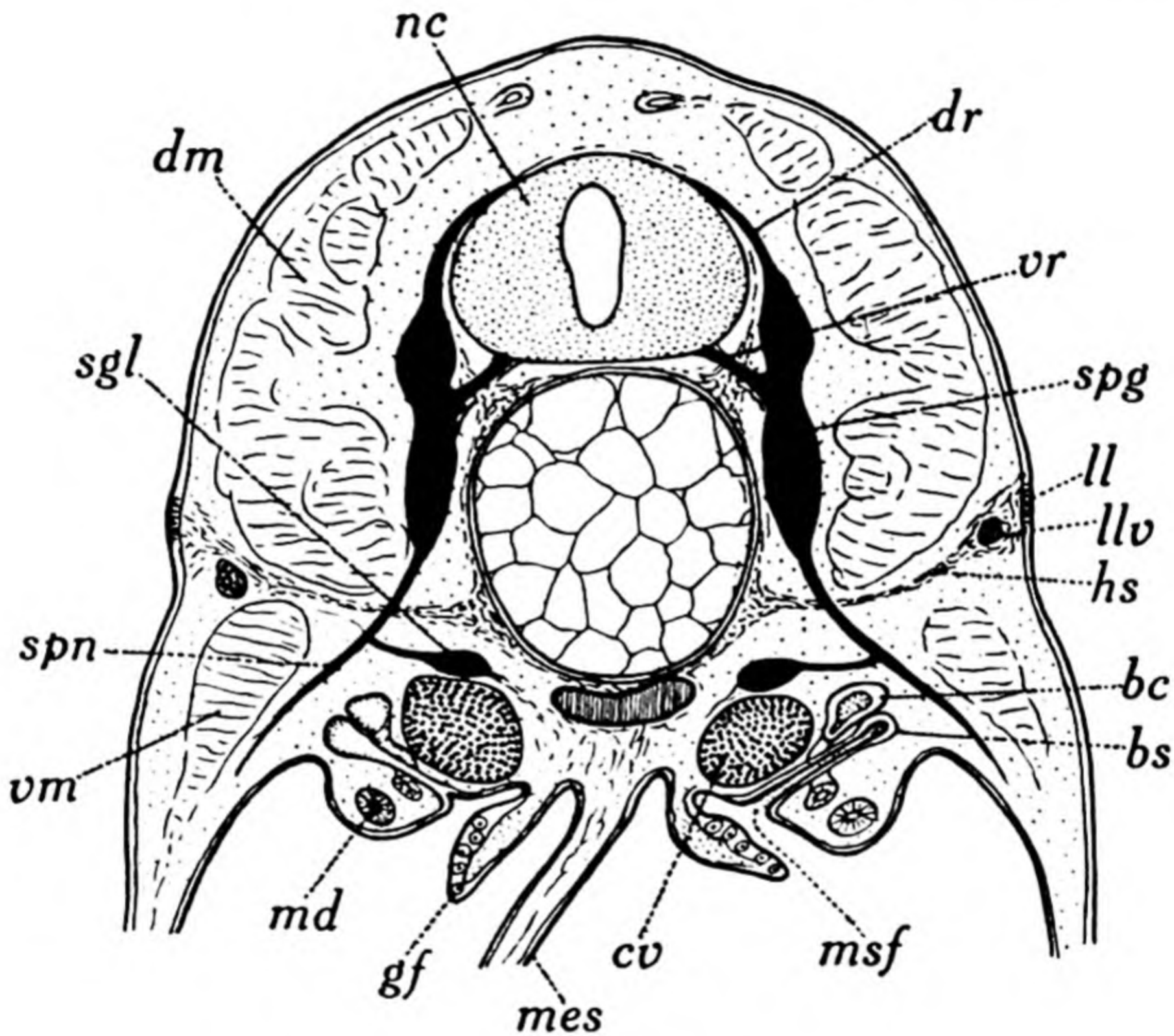
FIG. 669.

Thick transverse section of trunk of *Scyllium canicula* embryo 33 mm. long, showing spinal nerve and mesonephros. *bc*, Bowman's capsule; *bs*, blind sac at end of funnel tube; *cv*, posterior cardinal vein; *dm*, dorsal part of myomere; *dr*, dorsal root; *gf*, genital fold; *hs*, horizontal septum; *ll*, lateral line; *llv*, lateral-line vein; *md*, Müllerian duct (Wolffian duct just above it); *mes*, mesentery; *msf*, mesonephric peritoneal funnel; *nc*, nerve cord; *sgl*, sympathetic lateral ganglion; *spg*, spinal ganglion; *spn*, mixed spinal nerve (r. ventralis); *vm*, ventral part of myomere; *vr*, ventral root.

the posterior region of the latter often shows the same specialisations, though less pronounced. While the earlier observers (Rathke, 1833; Remak, 1855; Koelliker, 1861) believed the whole metanephros to be derived from branches of the ureter, the modern view of its double origin from the ureter on the one hand and nephrogenous blastema on the other was initiated by v. Kupffer in 1865, upheld by many authors since, and finally established by Schreiner (1053).

Excretory Organs of the Cyclostomata.—The kidney of adult Petro-

myzontia consists on each side of a longitudinal fold extending for about half the length of the splanchnocoele into which it hangs, and containing convoluted tubules more numerous than the segments. The tubules open into a longitudinal duct, situated at the free edge of the fold, and the right and left ducts join posteriorly to a median sinus leading to a pore at the tip of a papilla behind the anus, Fig. 98. Each tubule has a glandular
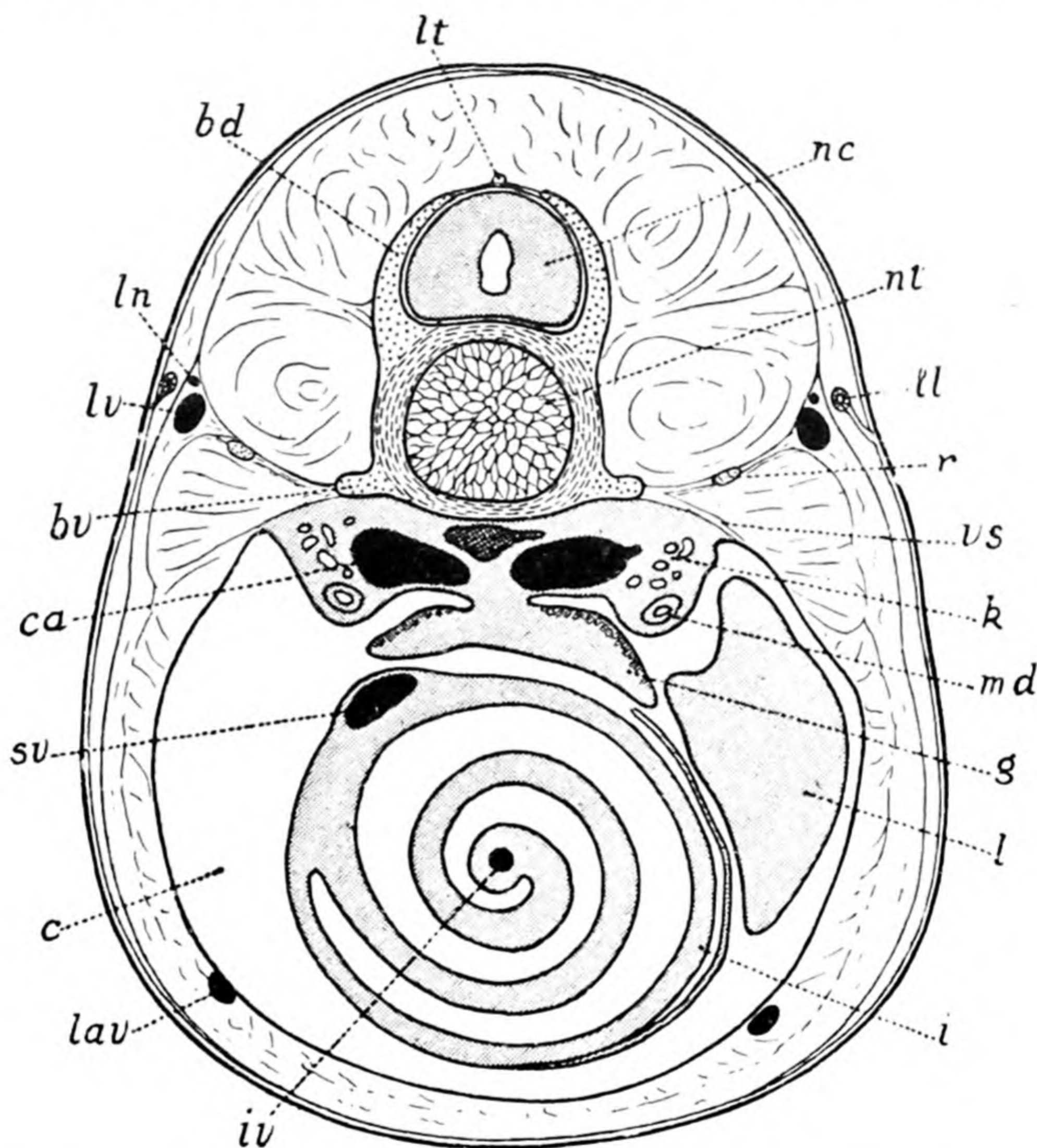
FIG. 670.

Scyllium canicula, late embryo ; transverse section of trunk. *bd*, Basidorsal ; *bv*, basiventral ; *c*, splanchnocoele ; *ca*, posterior cardinal ; *g*, genital ridge ; *i*, intestine ; *iv*, intestinal vein at edge of spiral valve ; *k*, mesonephros ; *l*, liver ; *lav*, lateral vein ; *ll*, lateral-line canal, and *ln*, its nerve; *lt*, longitudinal ligament ; *lv*, lateral-line vein ; *md*, Müllerian duct ; *nc*, nerve-cord ; *nt*, notochord *r*, rib in dorsal septum ; *sv*, supraintestinal vein ; *vs*, ventral septum.

portion and a typical Malpighian body with capsule and glomerulus ; but it is noteworthy that there are no peritoneal funnels. This kidney is a mesonephros similar to that of the Gnathostomes, Fig. 678.

The development of the renal organs has been studied by many observers since Rathke (1827) first described it in the Ammocoete larva (W. Müller, 1875 ; Schneider, 1879 ; Scott, 1054 ; Goette, 825 ;

Fürbringer, 1878 ; Vialleton, 1890 ; Bujor, 1891).   Recently a detailed account of the development of the pronephros and mesonephros has been given by Wheeler (1072), and by Hatta of the pronephros (1020a).

From six nephrotomes belonging to metaotic segments 4-9 arise six pronephric tubule rudiments as outgrowths of their parietal wall.   In
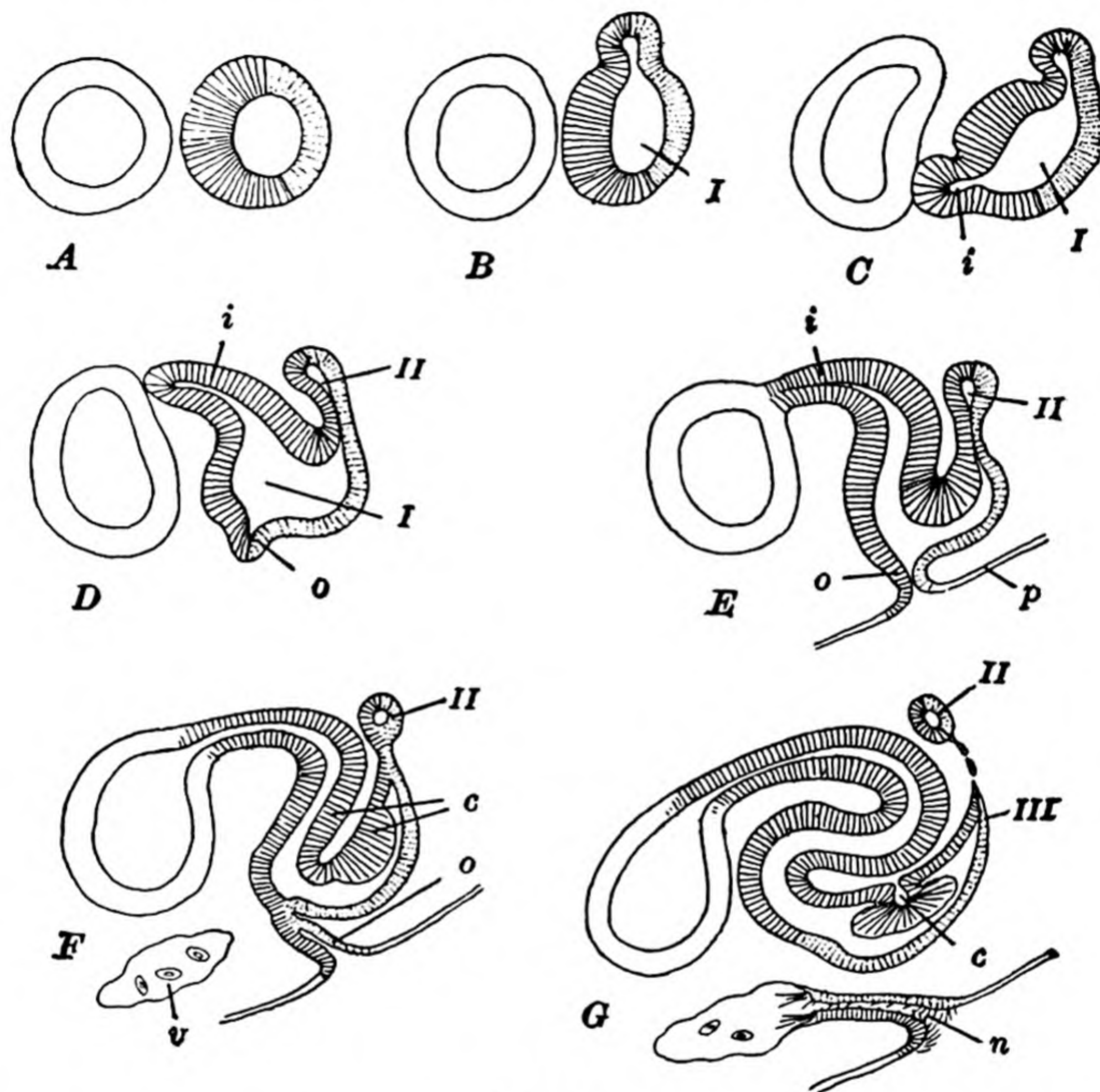
FIG. 671.

Series of diagrams illustrating development of primary mesonephric tubules in *R. sylvatica* (after Hall, from W. E. Kellicott, *Chordate Develt.*, 1913).   The Wolffian duct is drawn in outline simply ; mesonephric vesicles are shaded ; somatic part of tubule is shaded by continuous lines, splanchnic part by dotted lines.   A, Wolffian duct and simple mesonephric vesicle.   B, Mesonephric vesicle dividing into large primary mesonephric unit and small dorsal chamber.   The latter elongates antero-posteriorly and represents rudiment of secondary and later mesonephric units.   C, Formation of rudiment of inner tubule.   D, Inner tubule extending upward and toward mesonephric duct ; formation of rudiment of outer tubule.   E, Outer tubule fused with peritoneum and rudiment of funnel thus established ; Bowman's capsule forming ; commencement of differentiation of secondary meso-nephric tubules.   F, Separation of nephrostomal rudiment from remainder of tubule.   G, Connexion of funnel with branch of posterior cardinal vein ; separation of secondary tubule, and beginning of tertiary tubule indicated.   c, Bowman's capsule ; i, inner tubule ; n, peritoneal funnel ; o, outer tubule ; p, peritoneum ; v, branch of posterior cardinal vein ; I, primary mesonephric tubule ; II, secondary mesonephric tubule ; III, tertiary mesonephric tubule.

P. planeri, according to Wheeler, the five posterior rudiments develop into functional tubules ; but only the 3rd, 4th, and 5th do so in the species studied by Hatta.   The outer ends of these tubules bend backwards and join to form a longitudinal collecting pronephric duct.   Behind this region the duct is prolonged by the addition and fusion of segmental

rudiments which separate off from the successive nephrotomes (and appear to represent vestigial tubules) until it reaches the level of the cloaca. The duct then joins the wall of the cloaca and opens into its cavity at the junction between ectoderm and endoderm (p. 707).

It is to be noticed that the pronephric tubules arise from segments anterior to the ductus Cuvieri, and so are related to the anterior cardinal veins; also that the more anterior tubule rudiments extend into the branchial region. The larval functional organ begins just behind the last gill; its tubules become somewhat crowded backwards losing their segmental disposition, and project into the pericardial coelom where they open by conspicuous ciliated funnels. These are the nephrocoelostomes
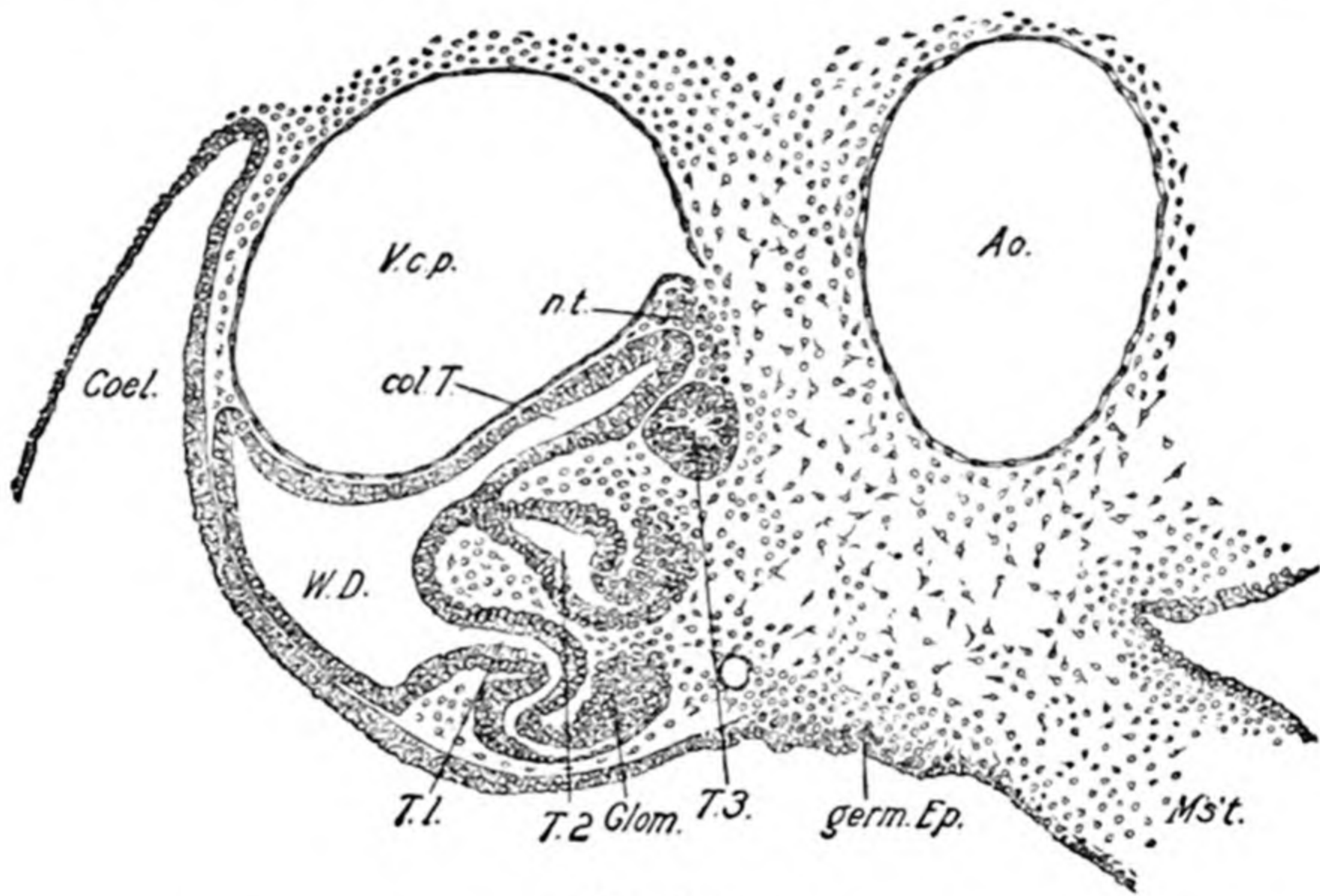
FIG. 672.

Transverse section through middle of Wolffian body of chick embryo of 96 hours (after F. R. Lillie, *Develt. Chick*, 1919). *Ao*, Aorta; *Coel*, coelom; *col.T*, collecting tubule; *Glom*, glomerulus; *germ.Ep*, germinal epithelium; *M's't*, mesentery; *n.t*, nephrogenous tissue; *T.1, 2, 3*, primary, secondary, and tertiary mesonephric tubules; *V.c.p*, posterior cardinal vein; *W.D*, Wolffian duct.

of segments whose nephrocoeles have opened out and become confluent with the pericardial cavity, and whose blood supply forms a glomus projecting into it, Figs. 522, 678. The pronephros atrophies at metamorphosis, its duct remaining in the mesonephric region.

Long before this atrophy the mesonephros has made its appearance further back in the nephric fold carrying the pronephric duct (Fürbringer, 1875; Vialleton, 1890; and especially Wheeler, 1072). The mesonephric tubules arise on the medial wall of this fold as thickenings of the peritoneum, which proliferate inwards, join and penetrate the wall of the duct. These cords of cells or tubule rudiments lengthen, separate off from the peritoneum, acquire a lumen, and expand at their inner ends into capsules into which blood-vessels are pushed, while their opposite ends open into the longitudinal duct. Thus each tubule has a Malpighian body, but no

peritoneal funnel. Doubtless the cells of the rudiments were originally derived from the nephrotomes, which, however, at this late stage have become broken up and scattered. The rudiments are not strictly segmental, in most of the mesonephric region number about six to a segment, and several may join to open into the duct.

More interesting and instructive are the structure and development
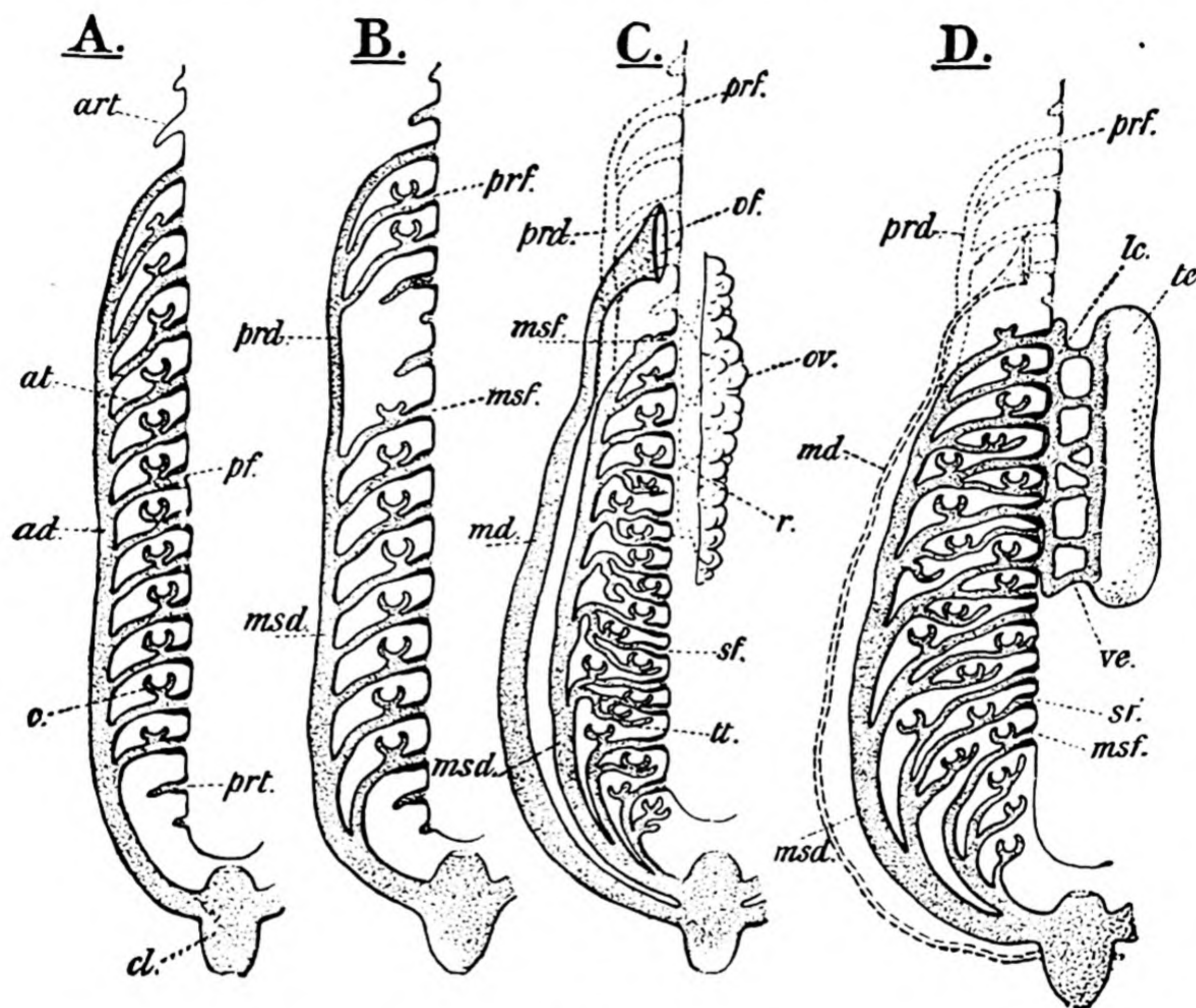
FIG. 673.

Diagrams of the urinogenital system in the Craniata. A, Hypothetical ancestral stage with continuous archinephros; B, Cyclostome with anterior pronephros; C, female Gnathostome (adult); D, male Gnathostome (adult). *ad*, Archinephric duct; *art*, anterior vestigial tubule; *at*, archinephric tubule; *c*, Malpighian capsule; *cl*, cloaca; *lc*, longitudinal canal; *md*, Müllerian duct; *msd*, mesonephric duct; *msf*, mesonephric funnel; *of*, coelomic funnel; *ov*, ovary; *pf*, coelomostome (funnel); *prd*, pronephric duct; *prf*, pronephric funnel; *prt*, posterior vestigial tubule; *r*, vestigial network of vasa efferentia; *sf*, secondary funnel; *te*, testis; *tt*, tertiary tubule; *ve*, vas efferens. The vestigial oviduct and the embryonic pronephros are represented by dotted lines in C and D. (From Goodrich, *Vert. Craniata*, 1909.)

of the renal organs of the Myxinoidea (J. Müller, 1836; Weldon, 1070; Maas, 1036; Spengel, 1065; Semon, 1061; Kirkaldy, 1034; Dean, 1003; Price, 1047; Conel, 1001). It is a remarkable fact that these Cyclostomes preserve the pronephros in adult life as an organ of considerable size projecting on each side of the oesophagus into the pericardial coelom (which retains a wide communication with the coelom of the

trunk on the right side). Each pronephros consists of a number of tubules opening on the one hand by very numerous branches ending in funnels (nephrocoelostomes) into the cavity of the pericardium and on the other hand into the remains of the longitudinal pronephric duct, Figs. 679, 680. The latter is degenerate and discontinuous, its communication with the more posterior mesonephric region being interrupted. The tubules are surrounded by blood-spaces and the latter may secondarily open into the duct (Conel, 1001 ; compare Anura, p. 669). Posteriorly is a glomus projecting into a chamber almost closed off. The function of this modified adult pronephros is probably in the main phagocytal.
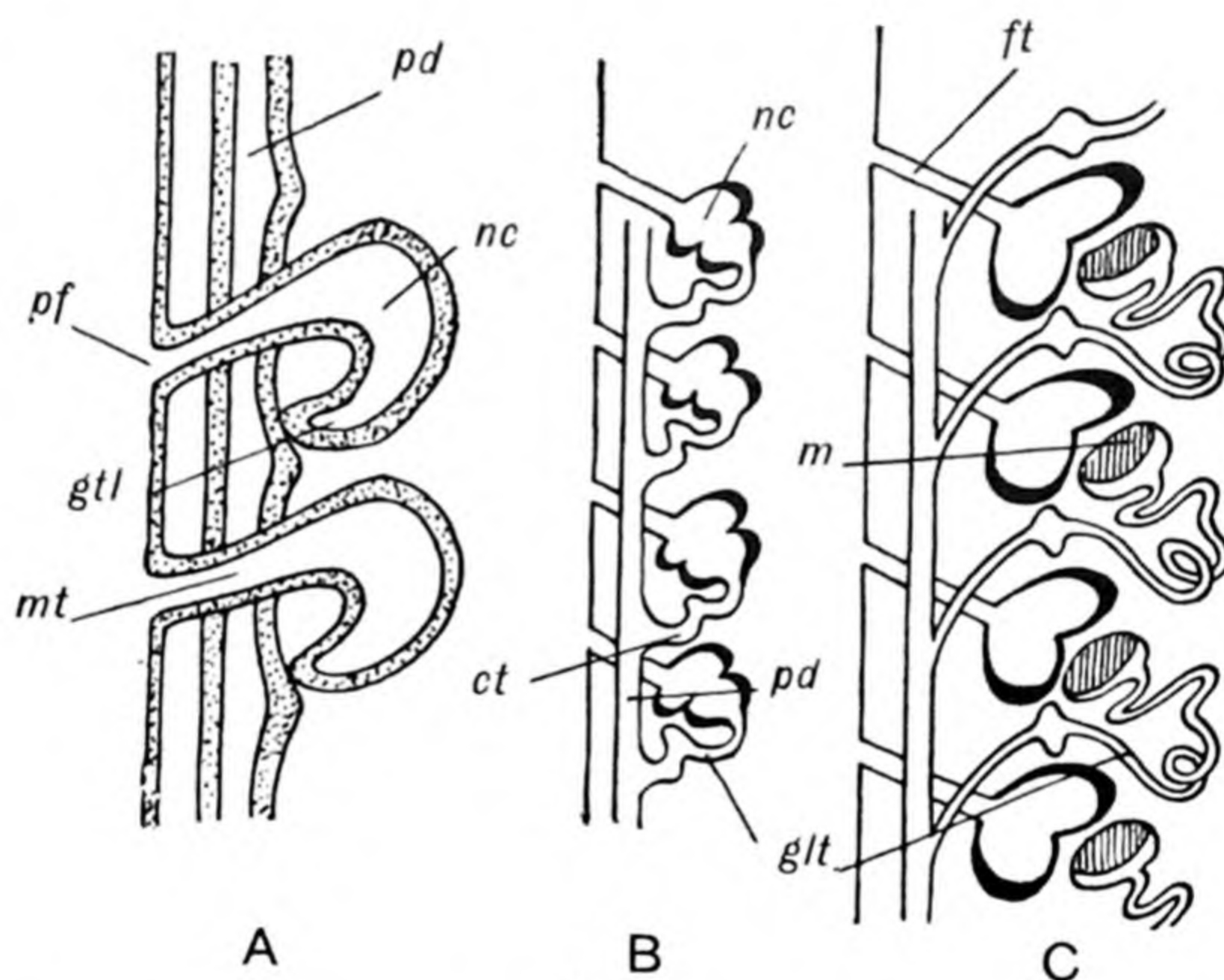
FIG. 674.

Diagrams illustrating development of mesonephros of *Squalus acanthias* (after J. Borcéa, 1905, from Ihle, *Vergl. Anat.*, 1927). A, Young stage showing blind end of primary tubule, *mt*, joining primary longitudinal duct, *pd*. B, Growth of nephrocoele chamber, *nc*, and of excretory collecting canal, *ct*. C, Separation of Malpighian capsule, *m*, from chamber. *ft*, Funnel canal; *glt*, glandular tubule; *pf*, peritoneal funnel.

The mesonephros extending along the whole length of the trunk coelom is no less remarkable, for it consists on each side of a longitudinal duct (former pronephric duct) provided with short tubules segmentally disposed, one pair to each segment. Each tubule ends blindly in a Malpighian body with capsule and glomerulus. The ducts open behind into the cloaca. The loss of peritoneal funnels is a sign of specialisation, but in other respects the mesonephros of Myxinoids is the most primitive known among Craniata, since it retains in the adult the presumably original strictly segmental disposition of the tubules and Malpighian bodies.

The early development is of great interest and has been well described by Price (1047) in *Bdellostoma*. The nephrotomes develop nephrocoeles

from about the 10th to the 80th segment of the trunk, and become some-what constricted, the middle portion forming the rudiment of a tubule and the outer thickened wall the rudiment of the longitudinal duct in each segment. From about segment 30 backwards the nephrocoeles become shut off from the splanchnocoele and give rise to Malpighian bodies ; but from about the 30th segment forwards the nephrocoeles, on
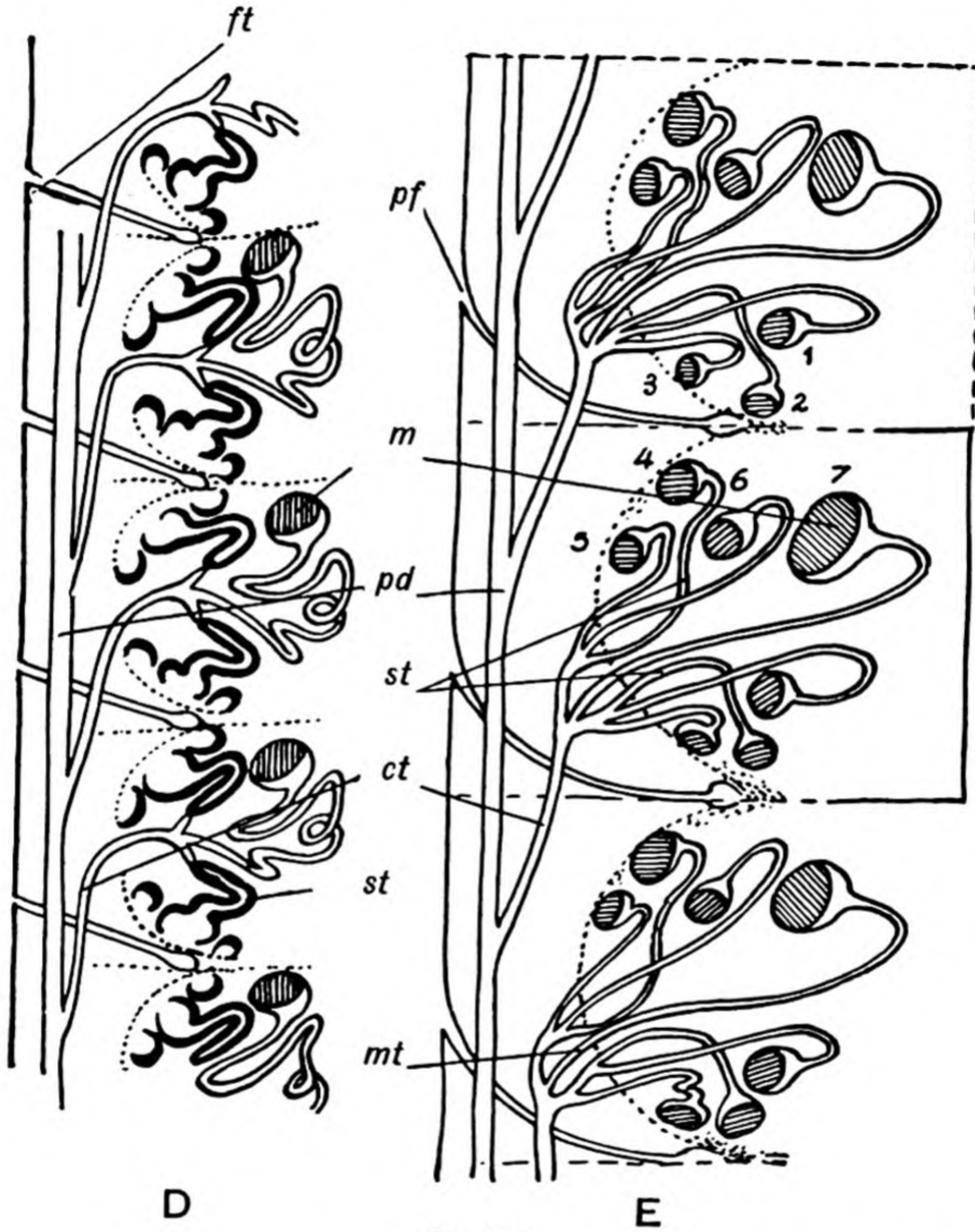
FIG. 675.

Diagrams illustrating late development of mesonephros of *Squalus acanthias* (after J. Borcéa, 1905, from Ihle, *Vergl. Anat.*, 1927). D, Growth from primary chamber of secondary chambers and canals. E, Opening of secondary capsules, derived from secondary chambers, into base of primary tubule, now collecting tubule (for lettering see Fig. 674).

the contrary, expand, fuse, and open out, merging with the general coelom, and in this region no glomeruli are formed. The limit between pronephros and mesonephros corresponds not to that between open and closed tubules, but occurs at about the 33rd segment where develops the pericardial wall. In front of this is formed the adult pronephros, composed of some three posterior closed and eighteen more anterior tubules all collected together,

and preserving open nephrocoelostomes. For, as the gill-sacs and heart move backward in development (Dean, 1003) the more anterior fifteen tubules are drawn backwards and crowded together, losing their original segmental disposition, and the duct is correspondingly shortened up.

As indicated above, the longitudinal duct is formed *in situ* by the coalescence of segmental contributions from each nephrotome along its course, its lumen being an extension of the nephrocoeles. Towards the posterior end where the duct opens into the cloaca (p. 710) the tubules are vestigial, and in about the last four segments the whole nephrotome is
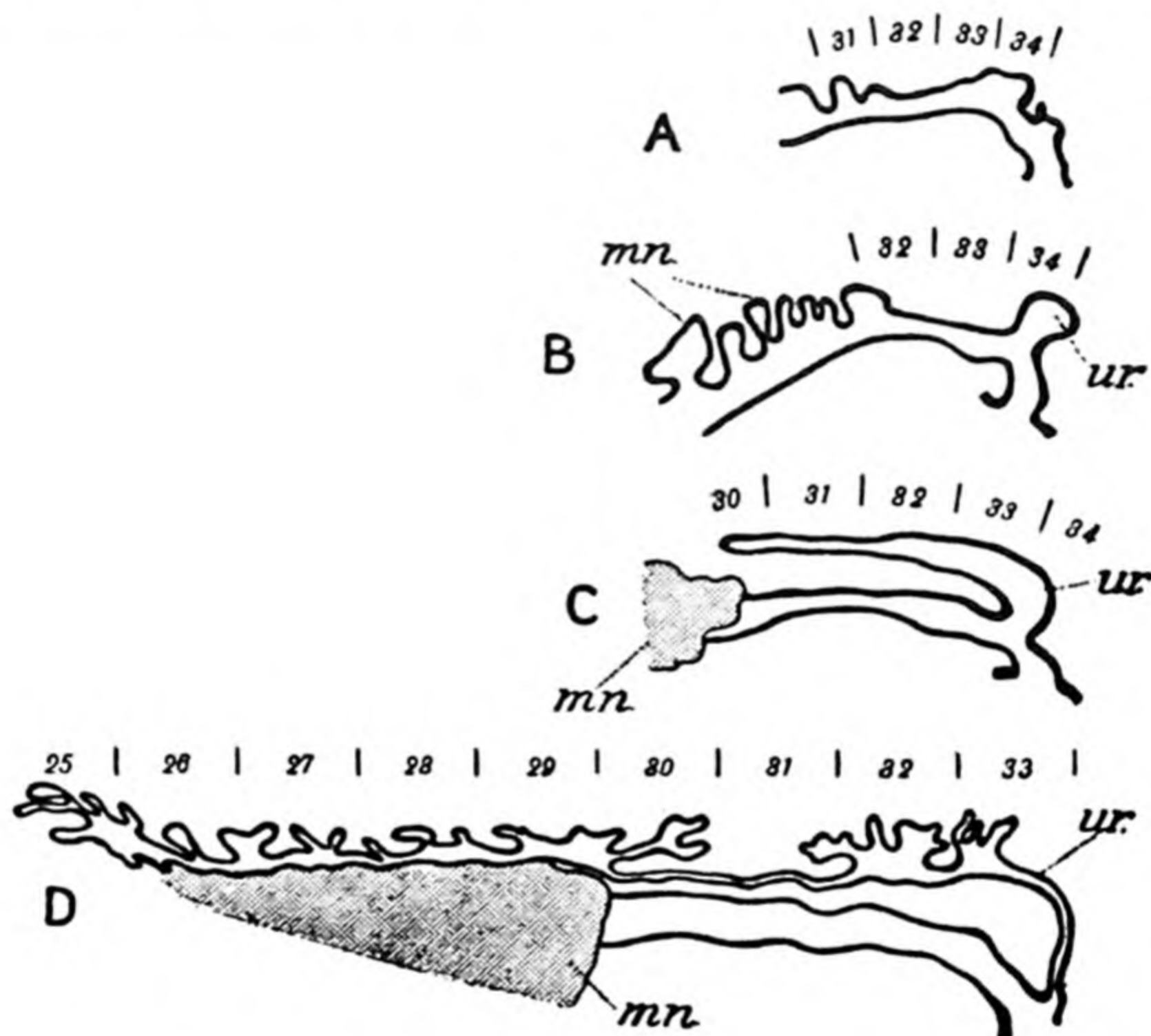
FIG. 676.

Reconstructed outlines of hind end of mesonephric duct and ureter in Bird embryos as seen from the left side. (After Schreiner, 1902.) A, Duck embryo with 48 segments; B, duck embryo with 50 segments; C, duck embryo, 10·75 mm.; D, fowl embryo, 13·5 mm. *mn*, Mesonephros; *ur*, ureter. The Arabic numerals indicate the position of the mesoderm segments. (From Kerr, *Embryology*, 1919.)

included in the formation of the duct. There are several points of importance to be noticed in the development of the excretory organs of *Bdellostoma* : (*a*) The tubules at first form a continuous uninterrupted segmental series ; (*b*) no secondary tubules are formed ; (*c*) the nephrocoeles of the more anterior tubules become confluent with the splanchnocoele (pericardial cavity), and the more posterior and greater number become closed capsules surrounding glomeruli ; (*d*) no peritoneal funnels persist ; (*e*) the limit between pro- and mesonephros does not coincide with that between open and closed tubules ; (*f*) only one longitudinal duct is developed on each side, and it is formed by the coalescence of segmental rudiments

from the nephrocoeles along its whole length ; (g) at first continuous, the duct becomes later interrupted between the pro- and mesonephric regions.

Distinction between Pro-, Meso-, and Metanephros.—Three different views have been held with regard to their general morphology. Gegenbaur, W. Müller, Koelliker, Fürbringer, held that they are three different, not homologous organs which replace each other completely. Sedgwick
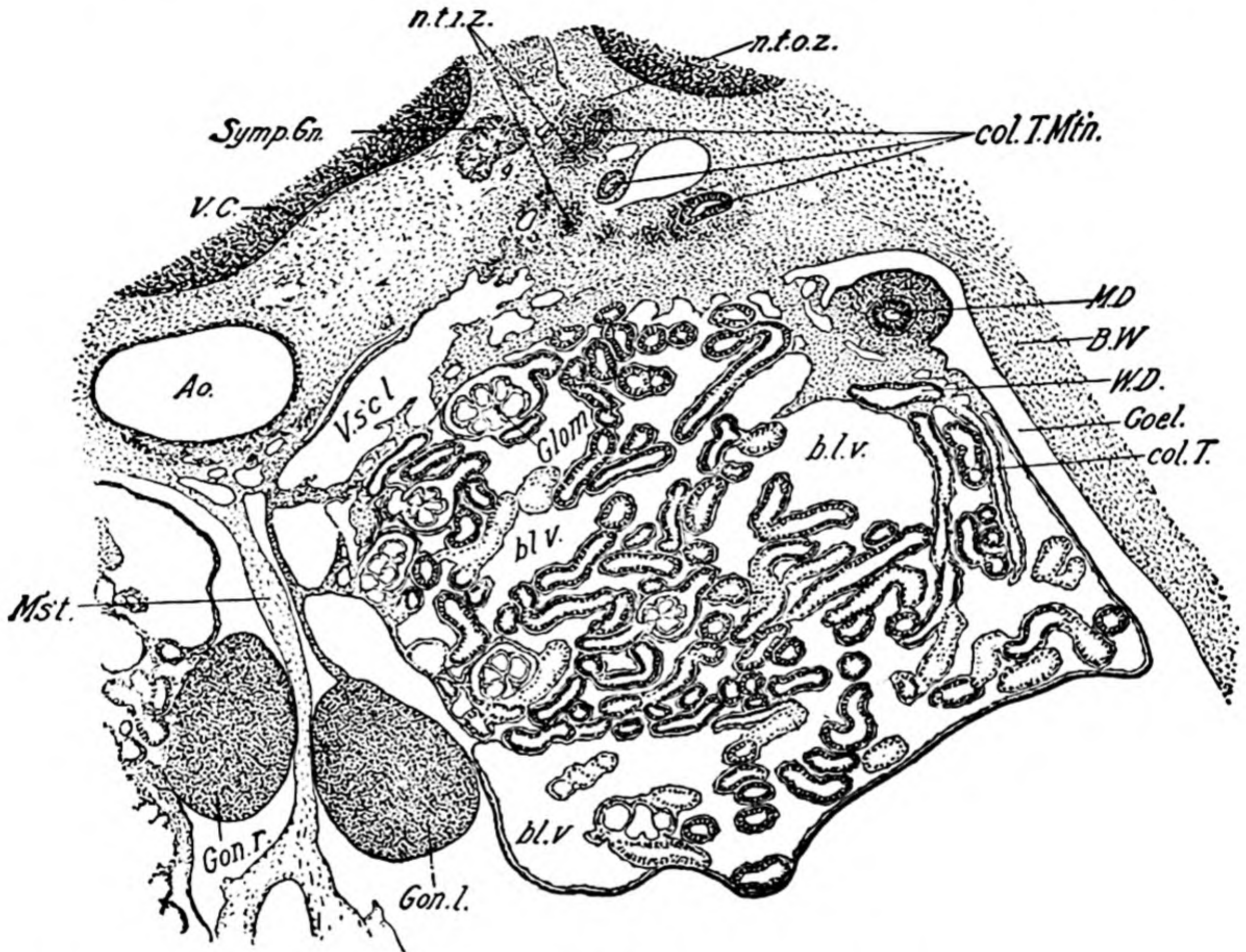
FIG. 677.

Transverse section through metanephros, mesonephros, gonads, and neighbouring parts of an 8-day chick (from F. R. Lillie, *Develt. Chick*, 1919). *b.l.v*, Blood-vessels (sinusoids) ; *B.W*, body-wall ; *col.T.M't'n*, collecting tubules of metanephros ; *M.D*, Müllerian duct ; *M's't*, mesentery ; *n.t.i.z*, inner zone of nephrogenous tissue (metanephric) ; *n.t.o.z*, outer zone of nephrogenous tissue ; *Symp.Gn*, sympathetic ganglion of twenty-first spinal ganglion ; *V.C*, centrum of vertebra. Other letters as in Fig. 691.

and Balfour, on the contrary, looked upon them as merely parts of one continuous organ, which develop successively from before backwards ; while Rückert held a somewhat intermediate view regarding them as three generations of similar tubules each more dorsal than its predecessor.

When the development of the mesonephros and metanephros was accurately worked out it had to be admitted that they are essentially of the same nature, and that the peculiarities of the metanephros are related to its late appearance and more specialised structure. The comparison

Nephrostomes

Pronephros

Glomerulus

Pronephric duct

Glomeruli
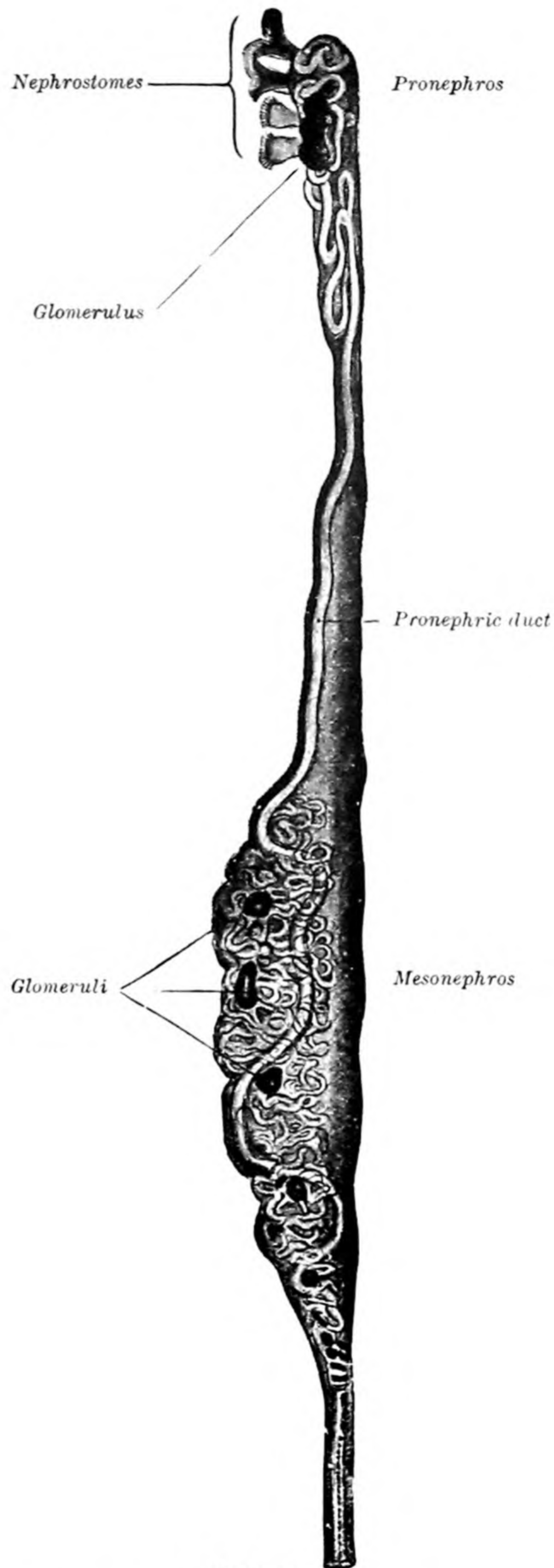
Mesonephros

FIG. 678.

The excretory system of a *Petromyzon fluviatilis*, 22 mm. in length, from the inner side. (After Wheeler.) About half the entire length of the primary urinary duct is represented, and behind the pronephros it is greatly coiled. Four pronephric funnels and a folded glomerulus are present, and between the pronephros and mesonephros is a portion wanting in tubules. (From Kerr, *Embryology*, 1919.)
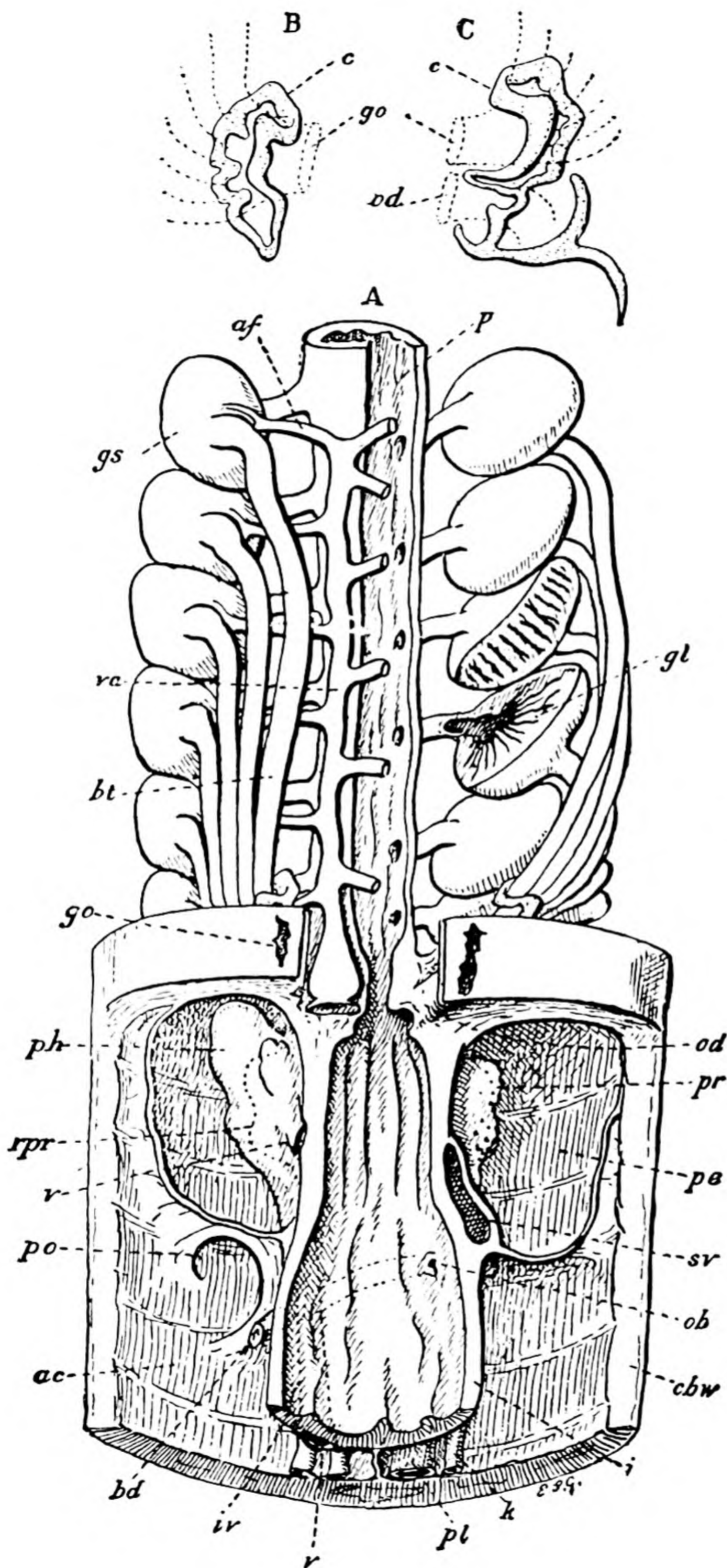
FIG. 679.

Myxine glutinosa, L.. A, Ventral view of a dissection ; B, cartilage near the opening of the right gill-pouches (indicated by dotted line) ; C, similar cartilage on the left side. *ac*, Abdominal coelom, exposed by cutting away ventral body-wall ; *af*, afferent vessel ; *bd*, bile-duct cut short ; *bt*, branchial tube leading to exterior ; *c*, cartilage ; *cbw*, cut body-wall ; *gl*, gill-lamellae exposed in gill-sac ; *go*, branchial opening ; *gs*, gill-sac ; *i*, intestine opened up ; *iv*, dotted line indicating course of portal vein ; *k*, kidney-duct ; *ob*, bile-duct opening ; *od*, oesophageal duct ; *p*, pharynx opened ; *pe*, pericardium opened—the heart has been removed ; *ph*, portal heart ; *pl*, left posterior cardinal vein ; *po*, opening from pericardial into abdominal coelom ; *pr*, pronephros ; *pr*, pronephros, with funnels on its surface ; *rpr*, dotted line indicating hidden right pronephros ; *sv*, sinus venosus cut across ; *v*, portal vein ; *va*, ventral aorta—the afferent vessels have been cut short on the left side, and the heart cut off behind the conus. (From Goodrich, *Vert. Craniata*, 1909.)

of the mesonephros with the pronephros is, however, not so easily made, and there is still much doubt as to the exact relation they bear to each other. The distinction once drawn between them as to structure (absence of peritoneal funnels, capsules, and glomeruli in pronephros) has broken down since Balfour described the pronephros of *Lepidosteus* and Brauer of *Hypogeophis*. It is also established that in both organs the tubules develop in essentially the same way from nephrotomes. Moreover, if it is true that secondary tubules are characteristic of the mesonephros and have never been proved to occur in the pronephric region, it must be remembered that they are totally absent in Myxinoidea, and that in any case this distinction is not fundamental. In many forms secondary
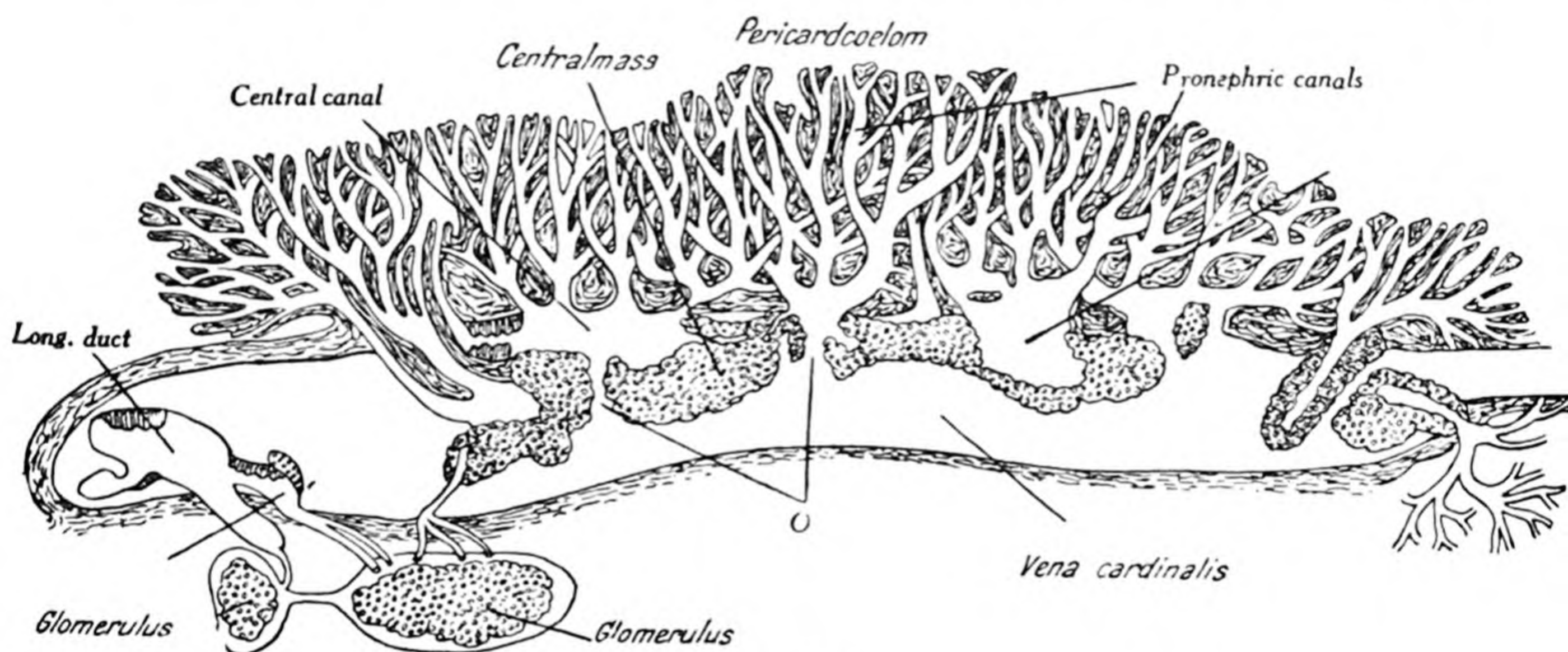
FIG. 680.

Reconstruction of 'head-kidney' of *Bdellostoma stouti* (after Conel, 1917; from Ihle, *Vergl. Anat.*, 1927). Pronephric tubules open by numerous branches into pericardial coelom; primary longitudinal duct interrupted, leaving short anterior 'central canal' disconnected from posterior longitudinal (mesonephric) duct; *O*, points at which pronephric tubules and central canal open secondarily into cardinal view.

tubules do not appear in several of the anterior segments of the mesonephros, Fig. 673.

Kerens has no doubt rightly insisted that there are no constant and fundamental differences in the development of the posterior pronephric and anterior mesonephric tubules of Amniota. Even the distinction, that, whereas the pronephric tubules are from the first continuous with the duct they help to form, the mesonephric tubules only secondarily fuse with it, breaks down; since a few of the posterior pronephric tubules may become connected with the duct in just the same fashion. The history of the tubules in *Bdellostoma* clearly shows that the anterior (pronephric) and posterior (mesonephric) are serially homologous organs which have diverged in structure in adaptation to different functions.

Moreover, the longitudinal duct is here derived all along its course from their outer ends. There can be little doubt that in Myxinoids pronephros
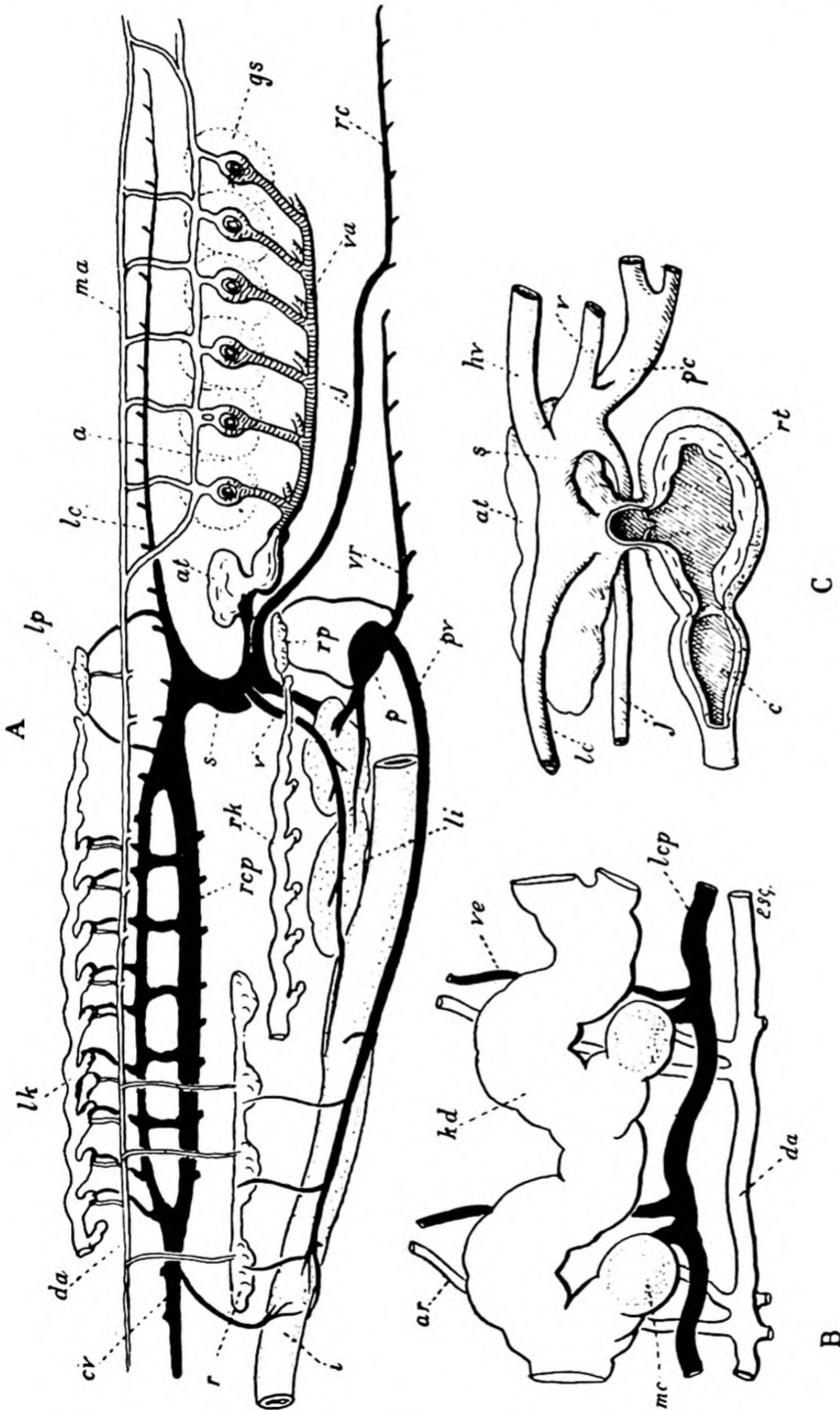
FIG. 680a.

A, Diagram of vascular system of *Bdellostoma*. B, Portion of *Bdellostoma*. B, Portion of kidney of *Bdellostoma dombeyi*, with its blood supply. C, Heart of same, with ventricle and conus opened (from Goodrich, 1909, modified). *a*, Paired anterior aorta; *ar*, segmental artery; *at*, atrium; *c*, conus separated by two valves from ventricle; *cv*, caudal vein; *da*, dorsal aorta; *gs*, gill-sac; *hv*, hepatic vein; *i*, intestine; *j*, jugular vein; *kd*, mesonephric kidney duct; *lc*, left anterior cardinal; *lcp*, left posterior cardinal; *li*, liver; *lk*, left mesonephros; *lp*, left pronephros; *ma*, median anterior aorta; *mc*, Malpighian capsule; *p*, portal heart; *pc*, united posterior cardinals; *pv*, portal vein; *r*, right ovary; *rc*, front end of right anterior cardinal; *rcp*, right posterior cardinal; *rk*, right mesonephros; *rp*, right pronephros; *rt*, cavity of ventricle separated by two valves from atrium; *s*, sinus venosus passing into left ductus Cuvieri; *sv*, intestinal vein; *va*, ventral aorta; *vr*, hinder end of right anterior cardinal.

and mesonephros represent two portions of an originally continuous and uniform archinephros with its archinephric duct; and it seems reasonable

to suppose that the same conclusion holds for other Craniates in which, however, a secondary multiplication of tubules has taken place posteriorly. The only serious difficulty attending this interpretation is presented by the mesonephric duct. For if it is really separated off from the nephrotomes all along its course (Petromyzontia, Urodela, Anura), it might be objected that the first generation of tubules had therefore been exhausted in its formation, that the usual development of the duct by free backward growth (Selachii, Amniota) represents the same process shortened up in ontogeny, and that the mesonephric tubules must consequently belong to a second series. But it seems more probable that the material which goes to form the duct in these forms only represents the outer ends of the tubules, temporarily separated off from their inner ends, which two regions later on again become connected together. We may suppose, then, that the original mode of formation of the duct is seen in Myxinoids and less clearly in *Petromyzon* and some Amphibia ; but that in other Craniates there has been an increasing tendency for the duct to be precociously developed while the tubules are delayed, and that backward free growth is merely a developmental device for the purpose.

Conclusion.—It may be concluded that the Craniata were originally provided throughout the trunk with a continuous series of segmental excretory tubules opening by peritoneal funnels into the coelom, and that by the growth backwards and coalescence of their outer ends they formed a longitudinal duct leading to the cloaca. Further, that such a primitive uniform archinephros no longer exists in any living form, but that owing to specialisation the series became differentiated into pronephric and mesonephric (opisthonephric) regions. Such a stage is represented in Myxinoids. The tendency for the pronephric tubules to develop early and to be replaced by later and more posterior tubules led to further specialisation of the pronephros, to the early completion of the duct before the mesonephric tubules developed, and their consequent secondary union with the duct. Instead of the duct being formed by the fusion of a succession of segmental rudiments, it tended more and more to be produced by the anterior tubules which grew freely back to the cloaca. Meanwhile, owing to the increasing importance of the mesonephros, the tubule-forming tissue (nephrotome) produced numbers of secondary tubules, and the original segmentation was lost.

THE GENITAL DUCTS OF GNATHOSTOMATA

Since the original function of the segmental tubules of the Vertebrata was probably to convey the spermatozoa and ova to the exterior (see p. 718), we might expect to find them still serving this purpose even in

the highest forms. Such indeed is the nature of the genital ducts in the male sex of all the Gnathostomes, though secondary specialisation may lead to considerable modification of their primitive structure.

The gonads develop in both sexes along paired genital folds, extending along nearly the whole length of the splanchnic coelom in primitive forms. The germ-cells develop chiefly on the outer (lateral) surface of each fold, but tend in higher forms to become more and more restricted to a short fertile region, while the anterior and posterior parts of the fold become sterile and degenerate. Now, it is an important fact that, while in the female sex the ova when ripe fall into the general splanchnic coelom (except in certain Actinopterygii, see p. 701), and are carried thence to the exterior usually by specialised ducts (p. 694), this primitive condition is never preserved in the male Craniata, except in Cyclostomes (p. 707). The testis of the male Gnathostome is always completely shut off from the general coelom (splanchnocoele), Fig. 681. The spermatozoa are never freely shed into this cavity, but are conveyed by a system of vasa efferentia to the primary mesonephric tubules and thence down the mesonephric duct to the exterior (see,
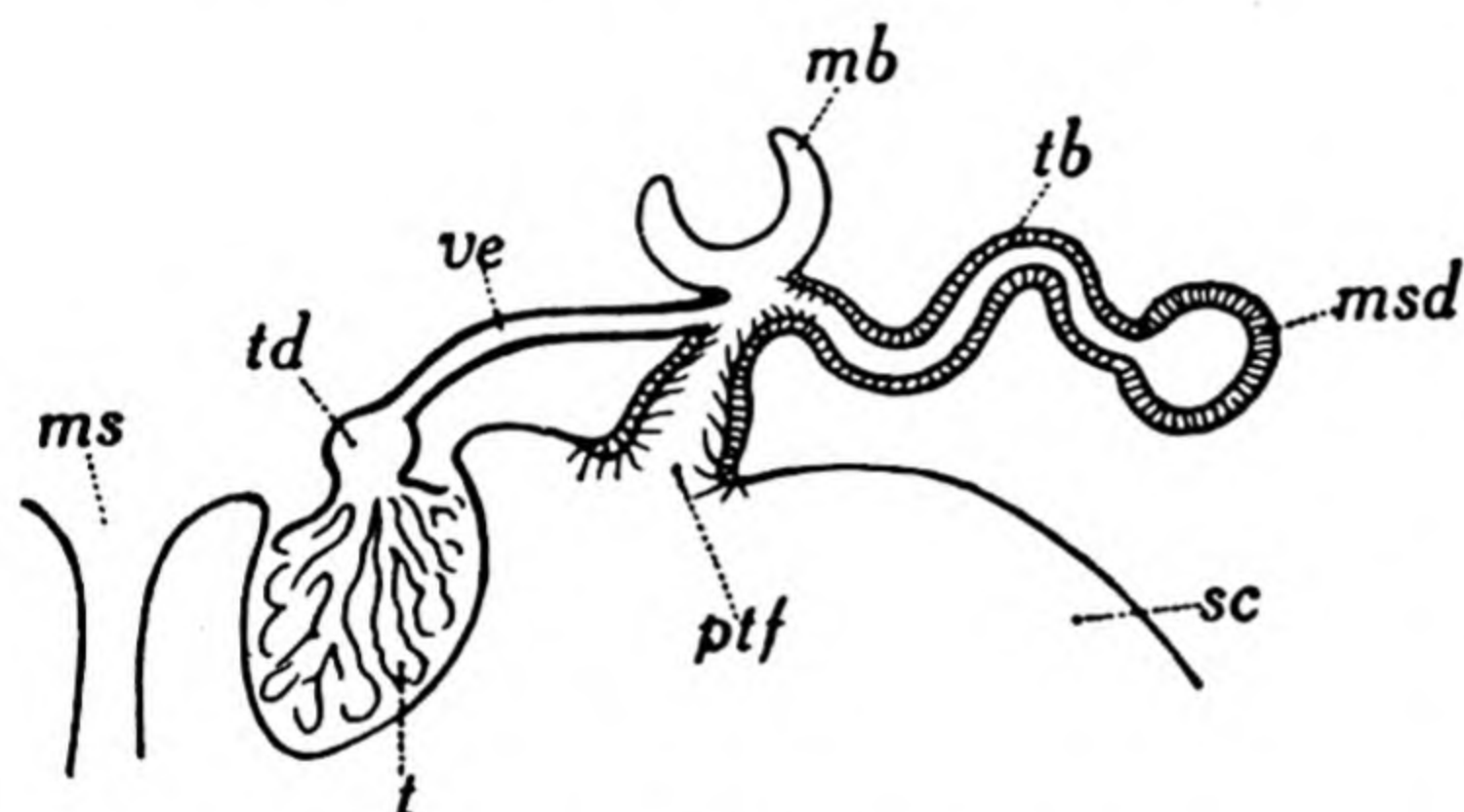
FIG. 681.

Diagram showing relation of mesonephric tubule to testis in *Gnathostomes* (except Selachian ?). *mb*, Bowman's capsule; *ms*, mesentery; *msd*, mesonephric duct; *ptf*, peritoneal funnel; *sc*, splanchnic coelom; *t*, testis with seminiferous tubules; *tb*, glandular tube; *td*, testis duct or marginal canal; *ve*, vas efferens.

however, secondary modifications in certain Osteichthyes described below).

In the more primitive condition, seen in *Acipenser, Lepidosteus, Amia,* and many Amphibia, the vasa efferentia extend across from testis to mesonephros along the whole length of the gonad. They usually join to form a longitudinal marginal canal (Nierenrandkanal of Felix), and while the transverse canals running from the marginal canal to the kidney are necessarily segmental since they open into the anterior primary mesonephric tubules, those passing from the testis to the marginal canal are usually more numerous, less regular, and frequently anastomose. There is a tendency for this anterior genital region of the mesonephros to lose its renal function, for its secondary tubules to degenerate, and for the posterior region to enlarge and take on the chief function of excretion.

In the various groups there is also a tendency for the vasa efferentia to become restricted to either the anterior or the posterior region of the testis, and for the tubules into which they open to become simplified by the reduction of the coiling and disappearance of the Malpighian body; Fig. 682.

The whole system of channels leading the spermatozoa into the kidney tubules, and known as the testicular network, may be considered as of originally coelomic nature and has probably arisen by
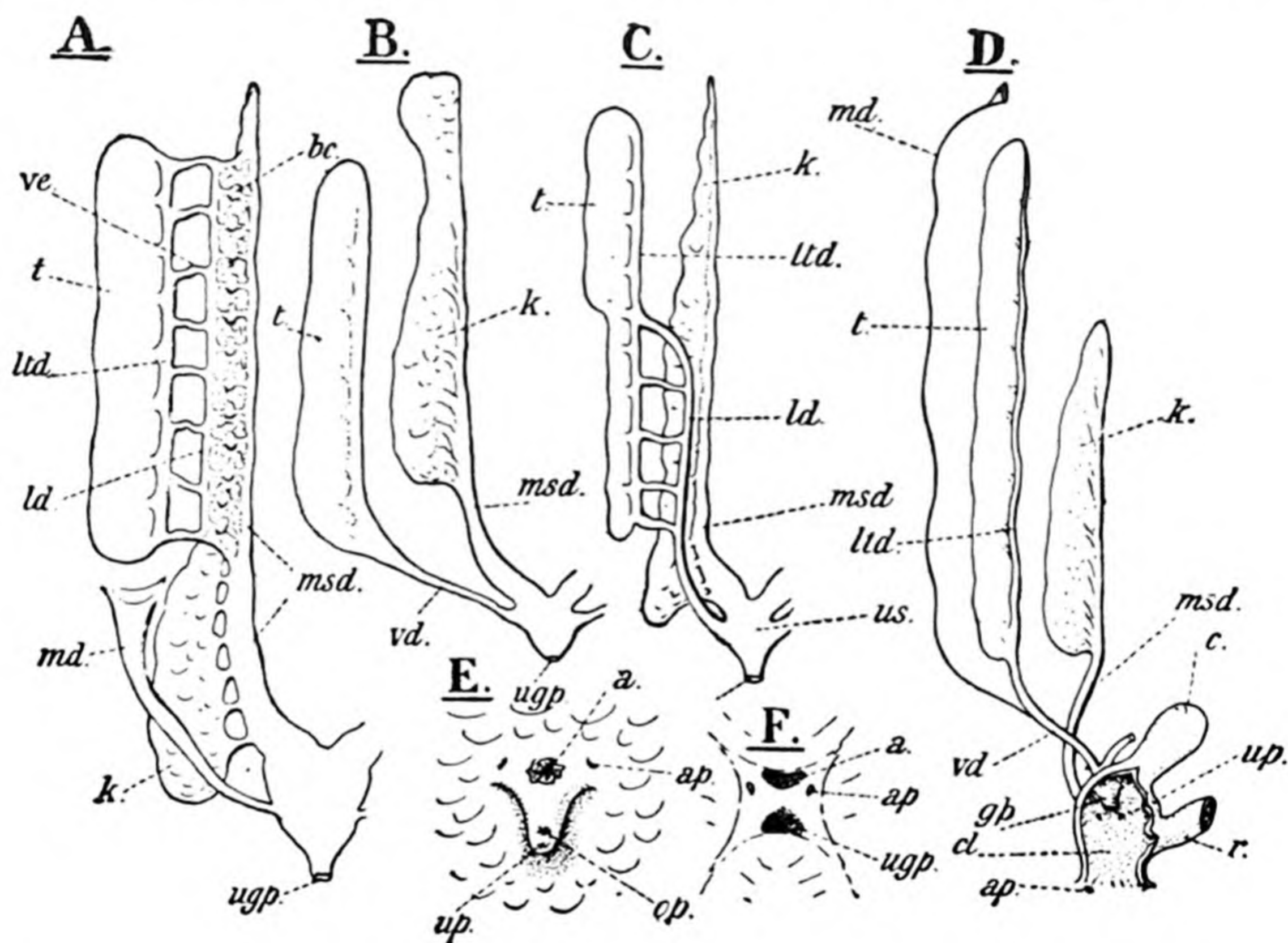
FIG. 682.

A, B, C, and D, diagrams of the urinogenital organs in male Dipnoi and Teleostomi. A, *Acipenser* (*Lepidosteus* and *Amia* are similar, but without the funnel, *md*) ; B, Teleostei ; and C, *Polypterus* (from Budgett's figures) ; D, *Protopterus* (from W. N. Parker's figures) ; E, urinogenital papilla of a female *Salmo*, ventral view ; F, similar view of a male *Polypterus* (after Budgett). *a*, Anus ; *ap*, abdominal pore ; *bc*, renal capsule ; *c*, cloacal bladder ; *gp*, genital papilla ; *k*, mesonephros ; *ld*, longitudinal duct ; *ltd*, longitudinal testis duct ; *md*, Müllerian duct ; *msd*, mesonephric duct ; *op*, oviducal pore ; *r*, rectum ; *t*, testis ; *ugp*, urinogenital pore ; *up*, urinary pore ; *us*, urinogenital sinus ; *vd*, vas deferens ; *ve*, vas efferens. (From Goodrich, *Vert. Craniata*, 1909.)

folds of the coelomic epithelium closing off ciliated grooves extending from the peritoneal funnels of the mesonephros to the genital fold. But the detailed homology of the various parts of the network is by no means thoroughly understood. The whole surface of the testis becomes covered by coelomic epithelium, while seminiferous tubules develop in its thickness; these open into a collecting or central longitudinal testis canal from which start the vasa efferentia, Figs. 673, 681.

In Elasmobranchs the testicular network is restricted to the anterior region of the testis, Fig. 684. The number of vasa efferentia may still be considerable in sharks, but in skates may become reduced to the most anterior one. The renal tubules of the genital region degenerate, and the twisted anterior part of the mesonephric duct (Wolffian duct,
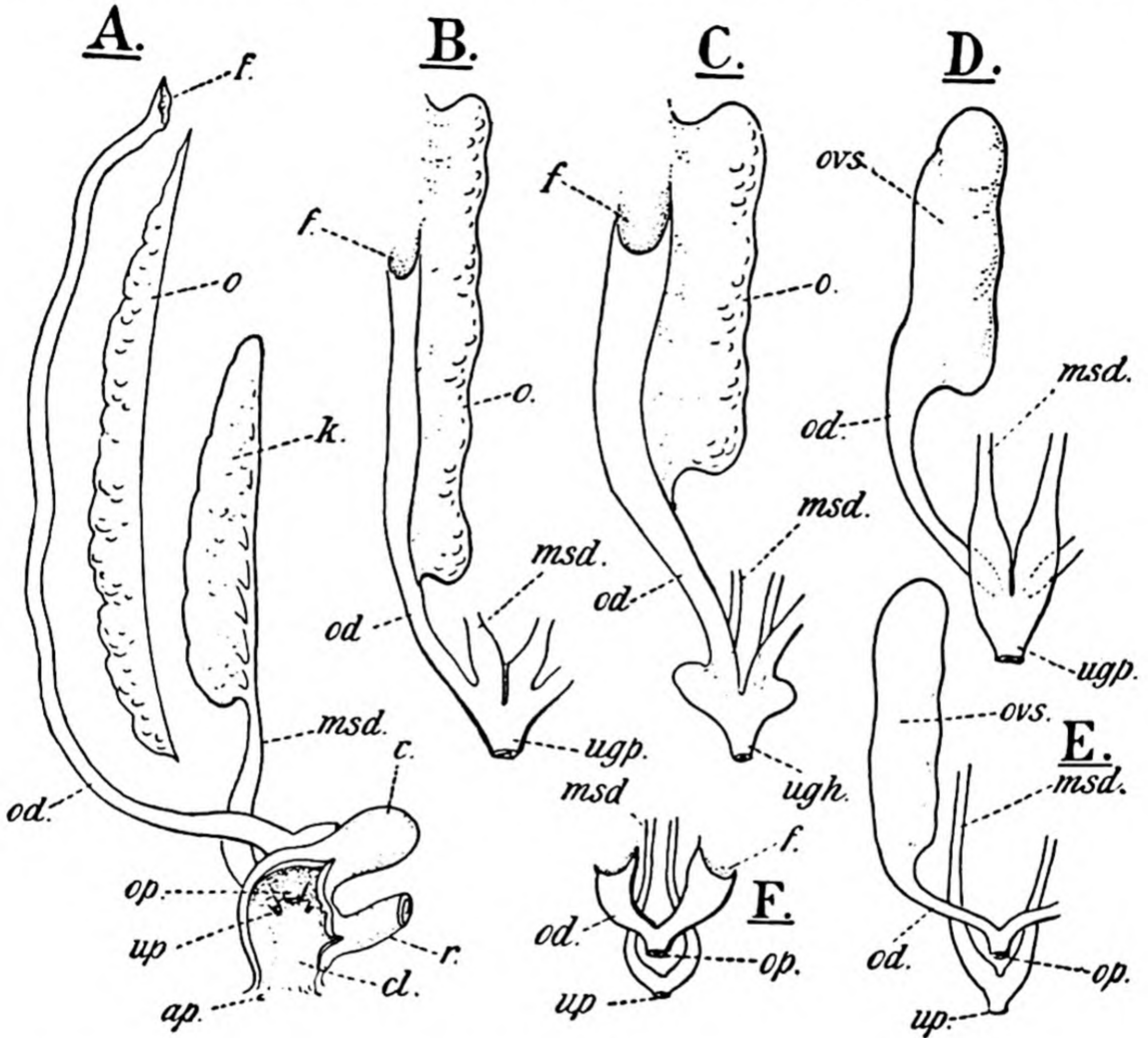
FIG. 683.

Diagrams of the female urinogenital ducts in the Dipnoi and Teleostomi derived from the figures of various authors. A, *Protopterus* (after Ayers and W. N. Parker); B, *Polypterus* (after Budgett); C, *Amia* (after Hyrtl and Huxley); D, *Lepidosteus* (after Balfour and Parker); E, a Teleost with closed ovisac; F, a Salmonid (after Weber). *ap*, Abdominal pore; *c*, cloacal bladder; *cl*, cloaca; *f*, open funnel of oviduct; *k*, mesonephros; *msd*, mesonephric duct; *o*, ovary; *od*, oviduct; *op*, genital papilla and pore; *ovs*, closed ovisac; *r*, rectum; *ugp*, urinogenital papilla; *up*, urinary pore. In all the figures, except F, only the right oviduct is completely drawn. (From Goodrich, *Vert. Craniata*, 1909.)

duct of Leydig), no longer renal in function, becomes glandular and secretes a white fluid (Semper, 1063; Balfour, 985; Borcéa, 991). The mesonephric peritoneal funnels which connect with the testis apparently reach its central canal into which they open (Balfour). Where it exists the longitudinal anastomosis or marginal canal appears to be derived from the capsules of the simplified Malpighian bodies (Borcéa). This is not the case in other fishes, such as Dipnoi, and

lower Teleostomes, where the funnels appear to reach no further than the marginal canal.[1]

The extension of the testicular network along the whole testis seen in primitive forms is modified in *Ceratodus* [2] and *Lepidosiren* where only
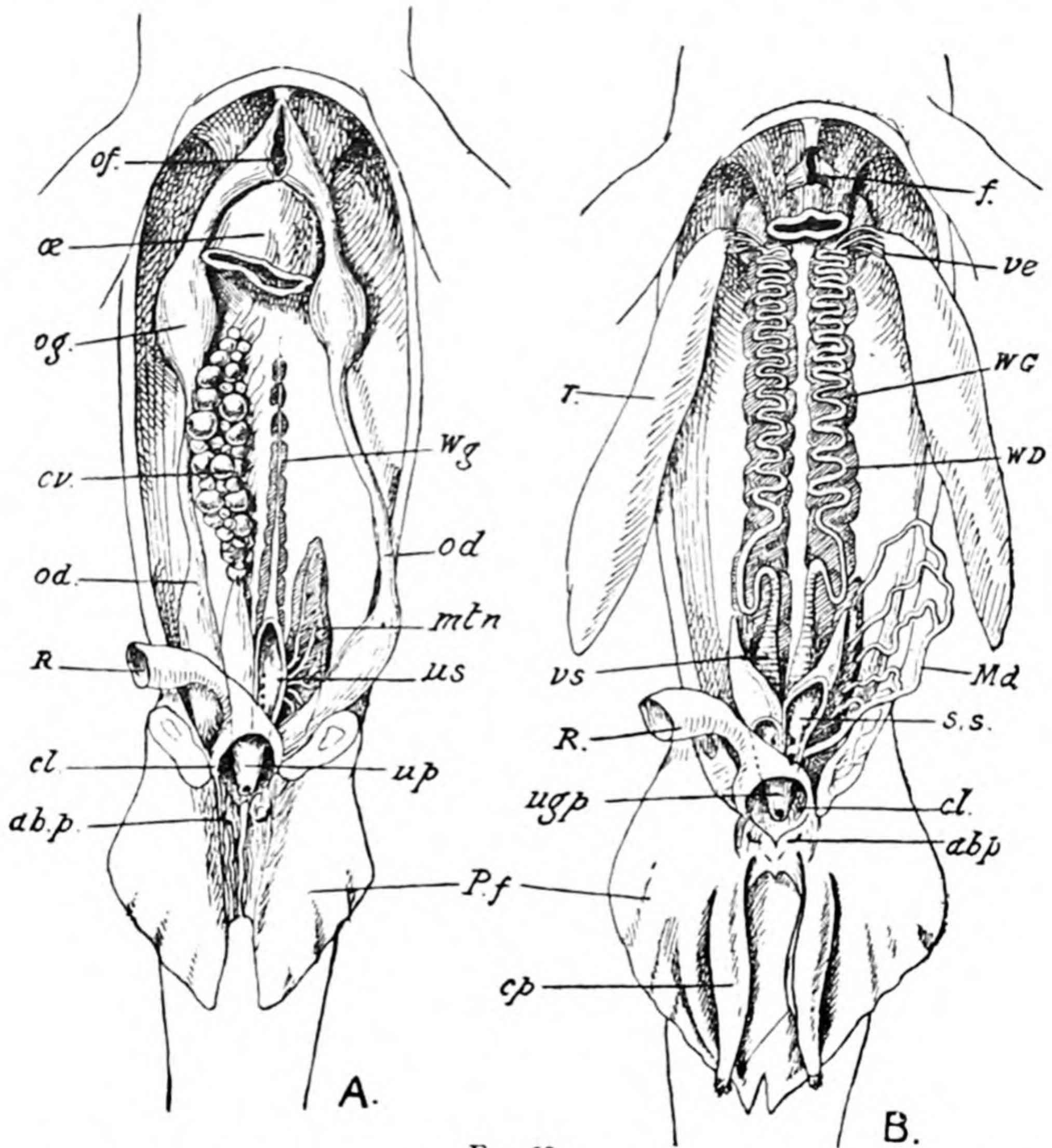
FIG. 684.

Scyllium canicula : urinogenital organs of female, A, and male, B, ventral view. *abp*, Abdominal pore ; *cl*, cloaca ; *cp*, clasper ; *f*, vestige of oviduct in male ; *Md*, ducts of posterior region of kidney (ureters) ; *mtn*, posterior excretory region of mesonephros (opisthonephros) ; *od*, Müllerian oviduct ; *oe*, cut end of oesophagus ; *og*, oviducal gland ; *ov*, ovary ; *P.f*, pelvic fin ; *R*, rectum ; *s.s*, sperm-sac ; *T*, testis ; *up*, urinary papilla in ♀ ; *ugp*, urinogenital papilla in ♂ ; *us*, urinary sinus ; *ve*, vasa efferentia ; *vs*, vesicula seminalis ; *WD*, Wolffian mesonephric duct ; *WG*, Wolffian gland or meso- nephros. (From G. C. Bourne, *Comp. Anatomy*, 1902.)

some half-dozen vasa efferentia persist at the hind end of the testis (Kerr, **1032** ; Semon, **1062** ; Ballantyne, **986**). In *Protopterus* they are still further reduced to a single canal leading from the degenerate sterile

[1] The exact relation of the testicular canals and marginal canal to the mesonephric tubules and peritoneal funnels has not yet been satisfactorily described in the various groups of Pisces.

[2] A detailed description of the urinogenital organs of Ceratodus is urgently needed.

tubular posterior region of the testis through the posterior mesonephric tubules to the base of the mesonephric duct (Kerr, 1032).

The Teleostomes show similar specialisations. While the more primitive forms, as mentioned above, have vasa efferentia all along the testis,
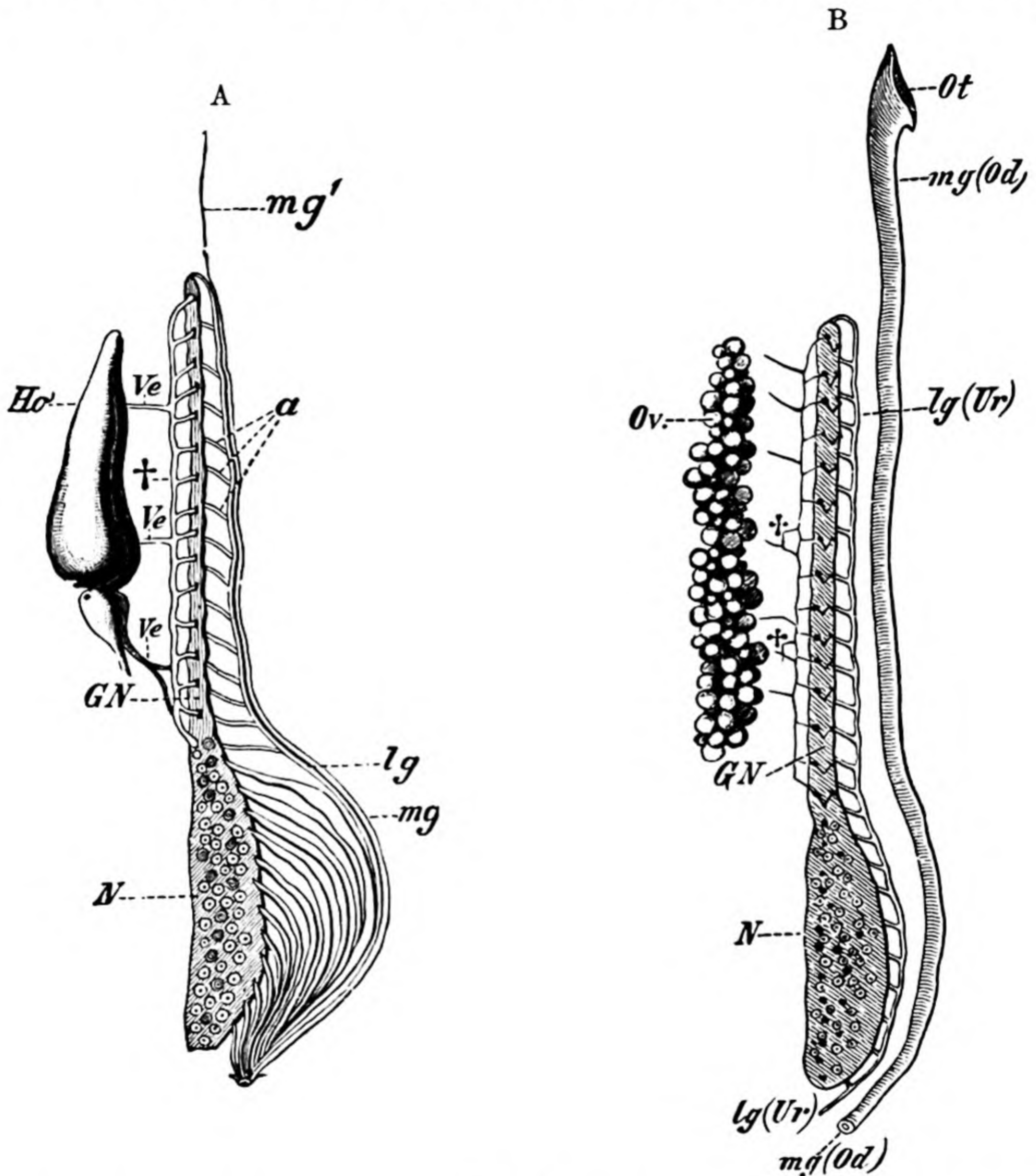
FIG. 685.

Diagram of the urinogenital system of (A) a male and (B) a female Urodele; founded on a preparation of *Triton taeniatus*. (After J. W. Spengel.) *a*, Collecting tubes of the mesonephros, which open into the Wolffian (urinogenital) duct (*lg*); in the female the latter serves simply as the urinary duct (*Ur*), and the system of the vasa efferentia (testicular network) is vestigial; *GN*, anterior portion of kidney (epididymis of the male); *Ho*, testis; *mg, mg¹*, Müllerian duct; *N*, posterior non-sexual portion of kidney; *Ot*, coelomic aperture of Müllerian duct (oviduct, *Od*); *Ov*, ovary; *Ve*, vasa efferentia of testis which open into the longitudinal canal of the mesonephros, †. (From Wiedersheim, *Comp. Anatomy.*)

in *Polypterus* (Budgett, 10; Kerr, 1033) the sterile posterior end of this organ consists of a collection of testicular canals leading to a single duct opening into the urinogenital sinus (base of mesonephric duct). The sperm thus no longer passes through the kidney at all, Fig. 682.

A structure of apparently similar origin is seen in the Teleostei (Kerr, 840). For in this group the testis is always quite separate from the kidney, and discharges its products usually into the base of the mesonephric ducts by a tubular prolongation which in some cases has been shown to be made up of testicular canals (Jungersen, 1028). The spermduct of the Polypterini and Teleostei is, then, to be interpreted as formed chiefly of the marginal canal which has grown backwards and come to open into the Wolffian duct separately from the kidney. Its opening into the duct may represent a single posterior tubule.

In Amphibia (Spengel, 1064) is also found an extensive testicular network in the more primitive Apoda and Urodela, with usually a well-developed marginal canal (Nierenrandkanal). But in Anura the network tends to become shortened, Figs. 681, 685-6.

The Amphibian network, however, is apparently of somewhat different structure from that of the fishes described above, since the primary peritioneal funnels open not into the vasa efferentia or marginal canal, but as usual into the splanchnic coelom. The transverse canals from the marginal canal communicate with the tubules at or near the capsules of the Malpighian bodies.

FIG. 686.

Diagram of a portion of the male generative apparatus in the Gymnophiona. *Ho*, Testis; *HS*, urinogenital duct; *K*, testicular capsules; *M*, Malpighian capsules; *N*, kidney; *Q*, transverse canals connecting the collecting duct with the longitudinal canal (*L, L*); Q^1, second series of transverse canals; *S*, convoluted portion of urinary tubule; *Sg*, collecting duct of testis; *ST*, nephrocoelostome. (From Wiedersheim, *Comp. Anatomy.*)

In ontogeny the whole network seems to arise from solid outgrowths of the capsules (Hoffmann, 1022; Semon, 1058-9; Gemmill, 1013). Except in Apoda the peritoneal funnels degenerate in the adult, and in Anura the Malpighian bodies as well.

The testicular network of the Amniota is doubtless built on the same plan as that of the Amphibia; but no open funnels persist, and they are usually only vestigial and closed even in development. The anterior region of the mesonephric duct, and the group of simplified tubules

derived from this end of the mesonephros and opening into the testicular canals, here constitute the epididymis of the adult.

There has been much difference of opinion concerning the homology of the network and the mode of development of its various parts in Amniotes. It is generally derived from a combination of ' rete-cords ' with ' sex-cords '; the former often appearing as solid rods of cells growing out of the capsules of Malpighian bodies, or directly from the coelomic
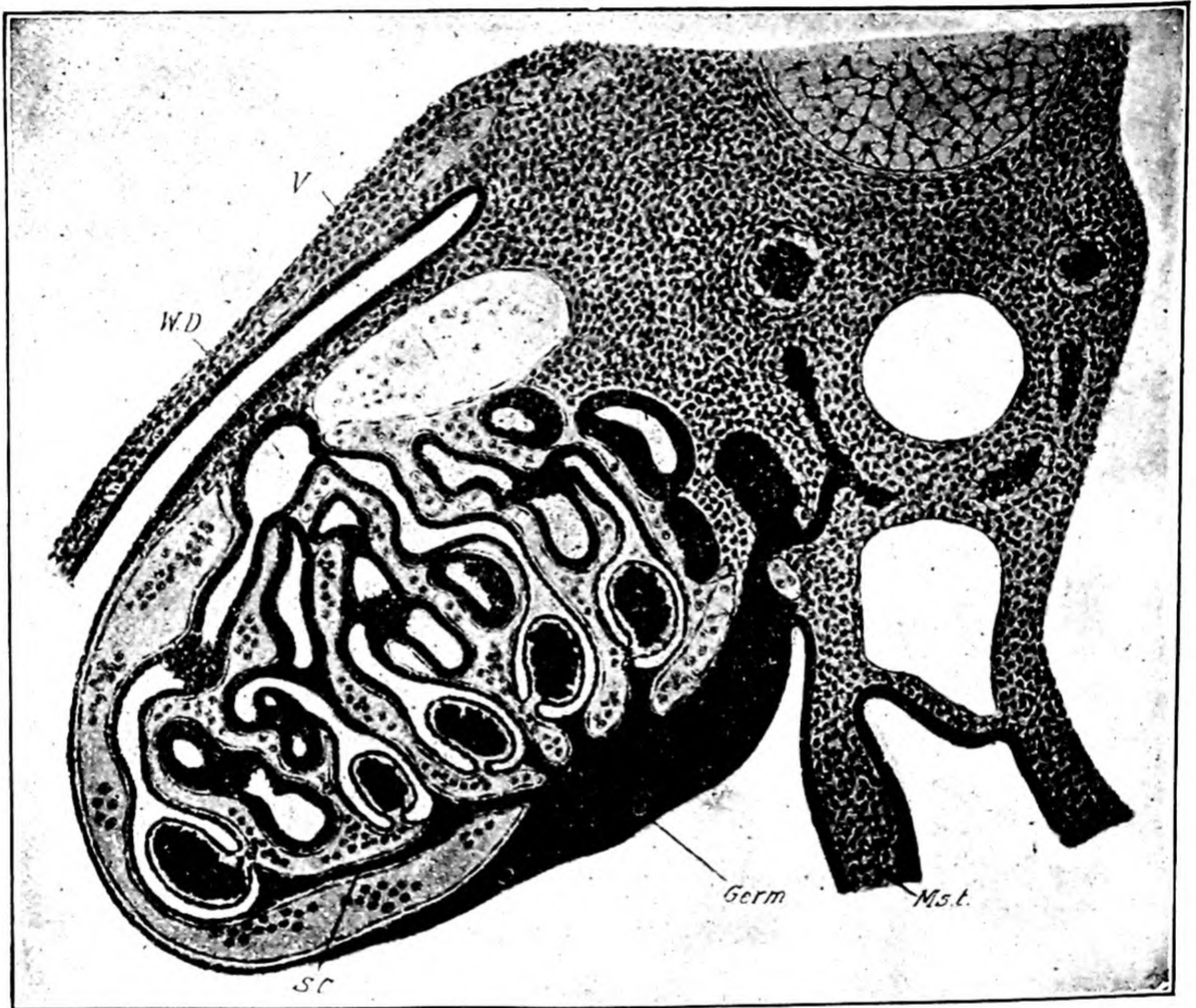
FIG. 687.

Cross-section through genital primordium of *Limosa aegocephala* (after Hoffmann, from F. R. Lillie, *Develt. Chick*, 1919). The stage is similar to that of a chick embryo of 4½ days. *Germ*, Germinal epithelium; *Ms.t*, mesentery; *S.C*, rete-cords; *V*, posterior cardinal vein; *W.D*, Wolffian duct.

epithelium, Fig. 687. The sex-cords are derived directly or indirectly from the epithelium of the genital ridge. As a rule these structures extend over more segments in young stages than in older (only those towards the middle persist to form the vasa efferentia), indicating that in Amniota also the genital region has been shortened and chiefly from behind. Both rete-cords and sex-cords are said to be derived from out-growths of the capsules by some authors (Braun, 1877–8, Weldon, 1071,

Hoffmann, **1022**, in Reptiles ; Semon, **1057** ; Hoffmann, **1022**, in the Chick ; Saimont, 1903, von Winiwarter, **1076**, in Mammals) ; while Janosik (**1027**) derived both from the coelomic epithelium.   Most observers
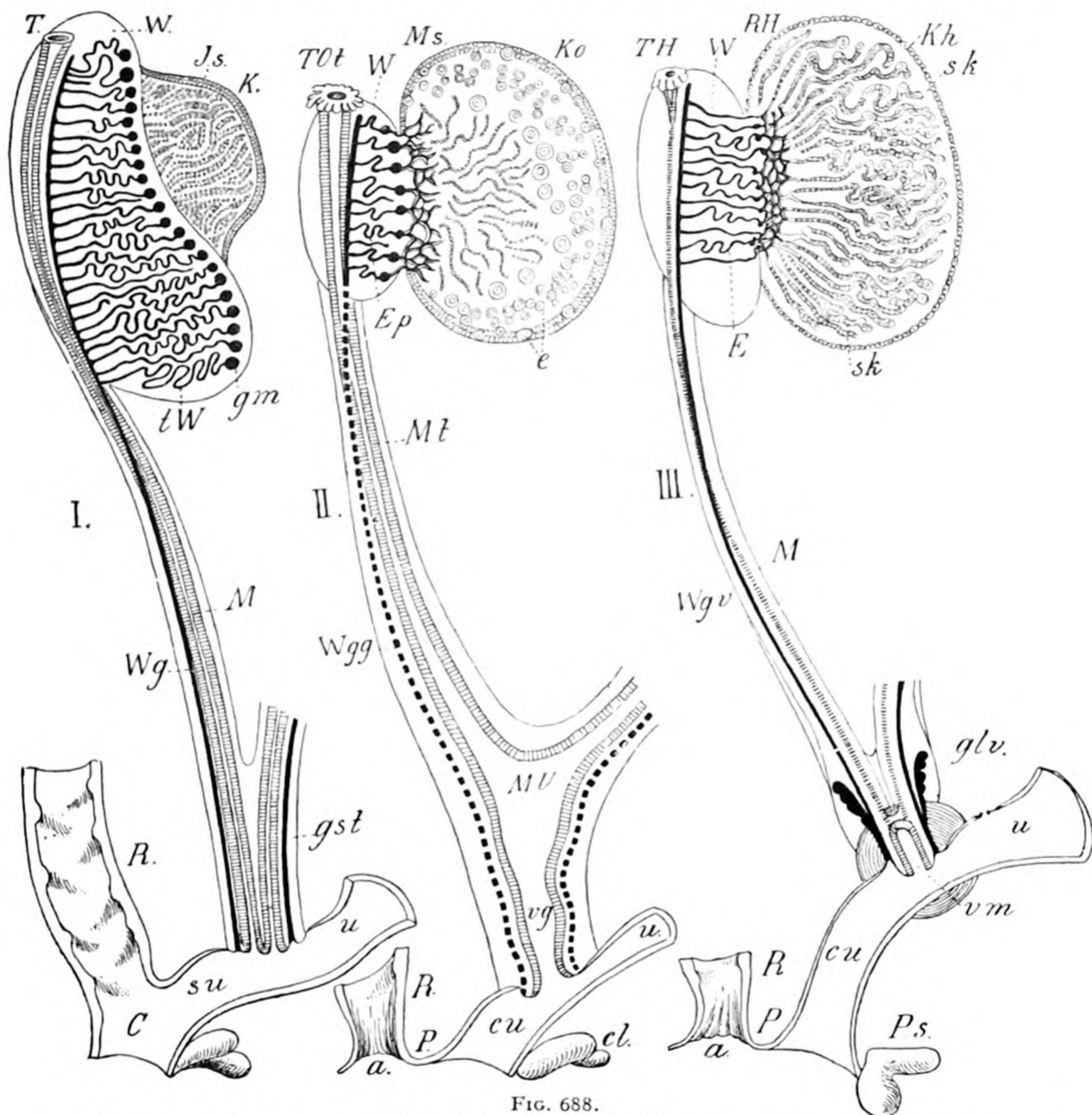
FIG. 688.

Diagrams of development and homologies of *Urinogenital system* in *Mammal*, omitting kidneys (after v. Milhalkovics, from M. Weber, 1927).   I., So-called indifferent stage, II., female, III., male. *a*, Anus ; *C*, cloaca ; *cl*, clitoris ; *cu*, urinogenital canal ; *e*, ova ; *E*, epididymis ; *Ep*, epoophoron ; *gm*, glomeruli ; *glv*, glandula vesicularis ; *gst*, genital cord ; *Js*, sex-cords ; *K*, germinal epithelium, *Kh*, of testis, *Ko*, of ovary ; *M*, *M.t*, Müllerian duct ; *MU*, uterus ; *P*, perineum ; *Ps*, penis ; *R*, rectum ; *RH*, rete Halleri ; *sk*, seminiferous canals of testis ; *su*, sinus urinogenitalis ; *T*, Müllerian funnel ; *Th*, hydatid of Morgan ; *Tt*, ostium abdominate ; *t.W*, mesonephric or Wolffian tubule ; *u*, urethra ; *vg*, vagina ; *vm*, vagina masculina (uterus masculinus) ; *W*, Wolffian body or mesonephros ; *Wg*, Wolffian or mesonephric duct = *Wgg*, duct of Gartner in ♀, and *Wgv*, vas deferens in ♂.

now agree that the rete-cords come from the capsules or the peritoneum just lateral to the genital ridge, and the sex-cords from the germinal epithelium (Milhalkovics, **1041**).   This conclusion is probably correct and

agrees best with the development of these parts in lower Gnathostomes, if we take the rete-cords to represent peritoneal funnel-canals leading to the capsules.[1] The observation of transient funnel-like structures joining the rete to the coelomic epithelium in the embryo of reptiles and mammals supports this interpretation (Allen, 981, in *Chrysemys*; Fraser, 1010, in Marsupials; Brambell, 994, in the mouse). In the higher mammals, however, these vestiges of funnels appear to be no longer recognisable (Allen, in pig, 980; Felix, in Man, 1006); and the rete-cords, then, have the appearance of prolongations of the sex-cords reaching the blind ends of the mesonephric tubules into which they eventually open, Figs. 688-9.

Our general conclusion with regard to the Tetrapoda is that the testicular network is formed by the combination of seminiferous tubules derived from the testis with mesonephric tubules originally provided with a peritoneal funnel opening into the splanchnocoele; that the junction of the two takes place in the region of the funnel-canal or capsule; and that, especially in the Amniota, the funnels themselves disappear more or less completely even in ontogeny. Anastomosis between the transverse vasa efferentia (Bowman's capsules ?) gives rise to a longitudinal marginal canal.

It is important to notice that the system of vasa efferentia, marginal canals, etc., in fact, the whole testicular network, is usually more or less completely developed in the female sex, though its vestiges may be much reduced in the adult, Figs. 685, 688.

The Müllerian Duct and Oviduct.—Besides the ducts described above, there exist in both sexes of Gnathostomes paired Müllerian ducts leading from the splanchnocoele to the exterior. They extend along the nephric folds, passing back on the outer side of the mesonephric duct (earlier archinephric duct), and primitively open in front close behind the septum transversum by a wide funnel into the coelom, and behind into the cloaca. They reach the front end of the cloaca by passing inwards ventrally to the mesonephric ducts. In the female sex the ova are shed into the splanchnocoele and are carried to the exterior by the Müllerian funnels and ducts; in the male the ducts are vestigial, apparently functionless, and rarely open into the cloaca. In spite of the general resemblance of these ducts throughout the Gnathostomes their phylogenetic origin is still obscure, and owing to their apparent absence in some forms (certain Teleostomes) and discrepancies in their development, their very homology has been doubted.

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[1] Such funnels represent the original communication of the nephrocoele with the splanchnocoele; but, owing to modifications in development, might easily appear as ingrowths from the coelomic epithelium towards or as outgrowths from the capsules.
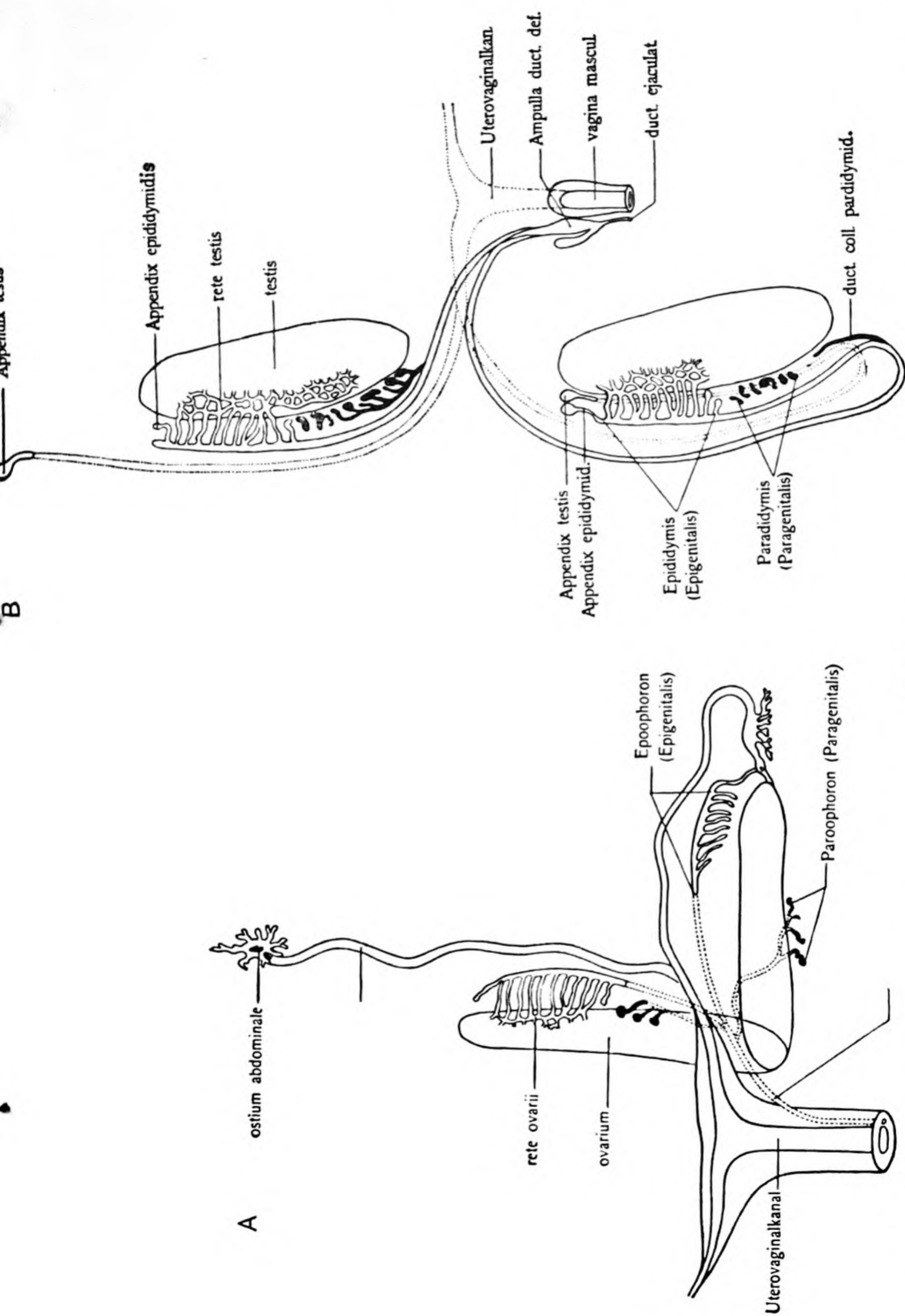
FIG. 689.

Diagrams illustrating fate of Mesonephros, Primary longitudinal duct, and Müllerian duct in human development of : A, female ; and B, male. Vestiges of posterior mesonephric excretory tubules in black (paroophoron, and paradidymis) ; more anterior tubules contribute to epigenital network ; while greater number of tubules still more anterior disappear. A, Ovary, though remaining in body-cavity, rotates through 90°. B, Testis wanders out of the body-cavity into scrotal sac.

All Tetrapoda are provided in the female with Müllerian ducts serving as oviducts,[1] Figs. 700-1. Their glandular wall secretes the albuminous covering and protective shell of the egg present except in some Marsupials and the placental Mammalia. Each duct opens in front by a wide 'ostium abdominale' or Müllerian funnel often provided with extensive ciliated lips drawn out in Mammals into fimbriated lobes. In the lower forms (Amphibia) the funnel retains its position far forward, Figs. 625, 685; but in others there is a progressive tendency for the duct to become shortened in the adult, and for the funnel to be drawn back to nearer the posterior region of the coelom of the trunk, especially in Mammals. In the Placental Mammals the two ducts fuse
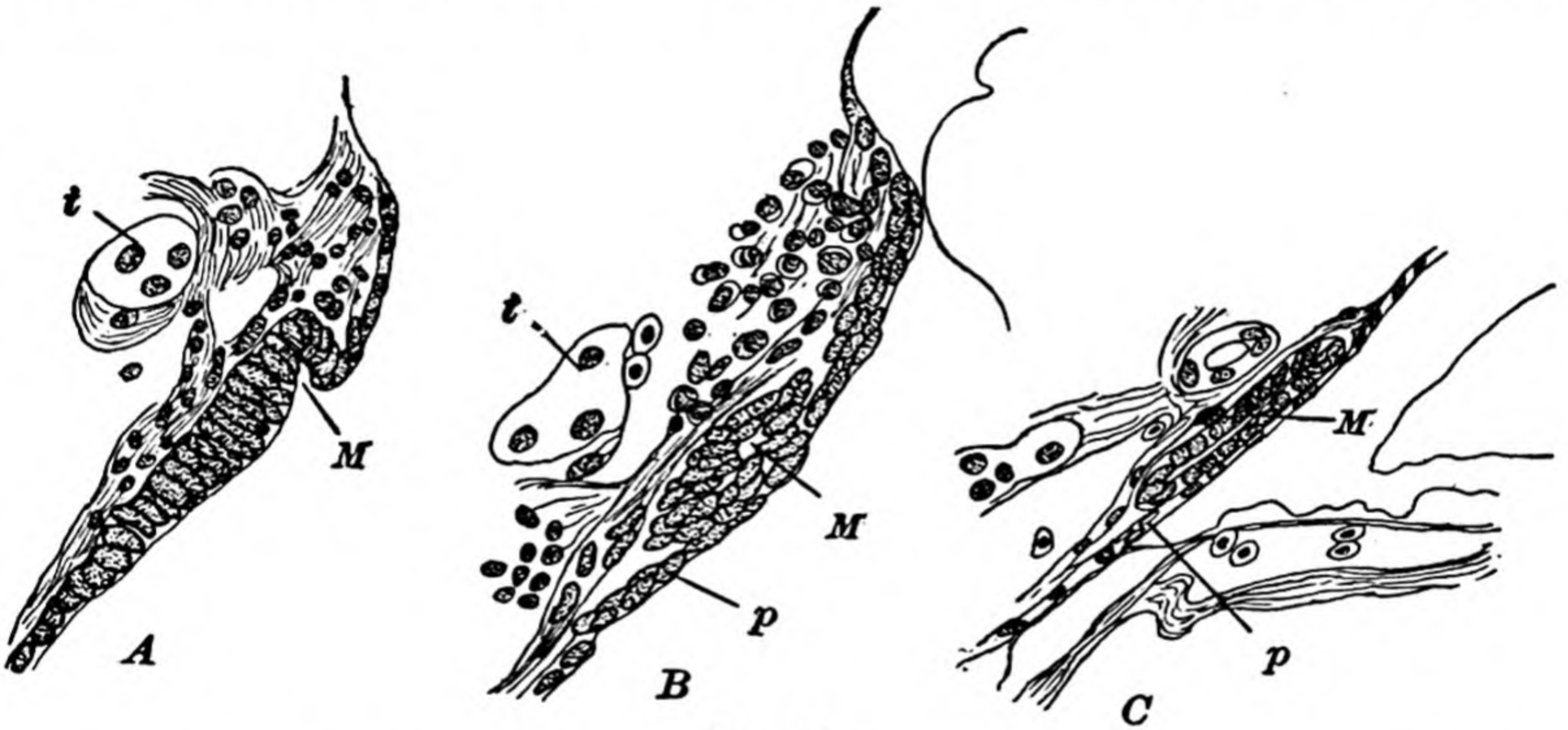
FIG. 690.

Sections through developing Müllerian duct of a 34 mm. tadpole of *R. sylvatica* (after Hall, from W. E. Kellicott, *Chordate Develt.*). A, Section passing through beginning of Müllerian evagination. B, Section posterior to A; duct established but still connected with peritoneum. C, Section still farther posterior, showing separation of duct from peritoneum. M, Müllerian duct; p, peritoneum; t, third pronephric tubule.

to a median vagina at their base, and in the higher groups their swollen uterine regions may also fuse to a median uterus.

Concerning the development of the Müllerian duct in the Tetrapoda there has been much controversy and the question cannot yet be considered as definitely answered. Balfour and Sedgwick maintained that in the chick the funnel is derived from the pronephros and the duct itself is split off from the archinephric (primary or Wolffian) duct. Most of the earlier observers believed this to be the usual mode of development of the Müllerian duct in Amniotes. In adopting this interpretation they were doubtless influenced by the fact that such had already been shown

[1] It has long been known that as a rule in Birds only the left ovary and oviduct are fully developed and functional in the adult. The left oviduct early ceases to grow and the left ovary likewise becomes atrophied. Occasionally these organs may be developed on both sides (Gadow, 1912).

to be the origin of the Müllerian duct in Selachians (Semper, 1063; Balfour, 317).

But it seems now to have been satisfactorily established by later workers that, at all events in Amniotes, the Müllerian funnel is developed by the closing over of a groove on an area of thickened epithelium (funnel area) situated at the edge of the anterior end of the nephric folds, and passing back along the lateral surface of the mesonephros towards the cloacal region as a longitudinal band of thickened coelomic epithelium
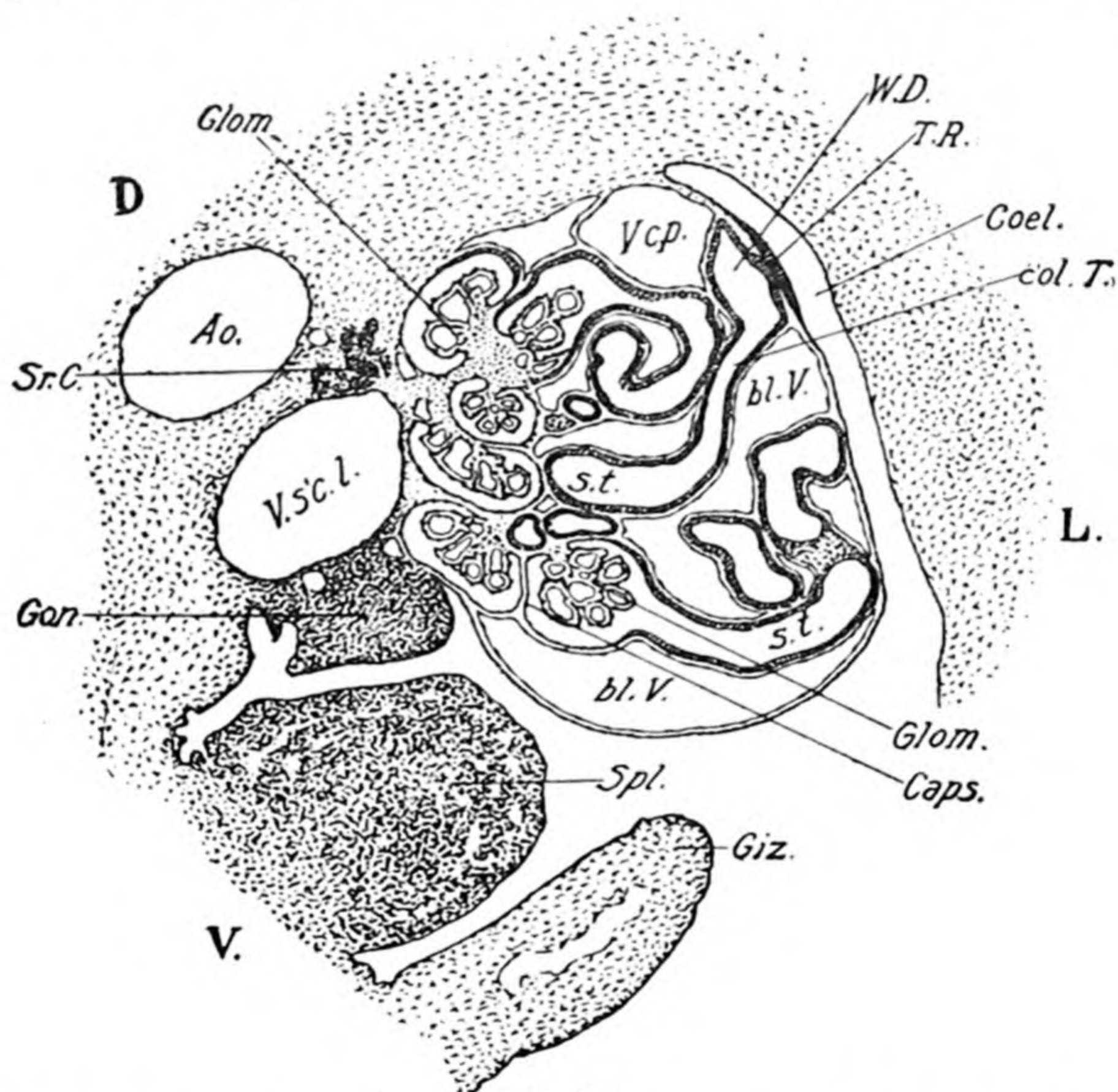
FIG. 691.

Transverse section through mesonephros and neighbouring parts of a 6-day chick, in region of spleen (from F. R. Lillie, *Develt. Chick*, 1919). *Ao*, Aorta; *bl.V*, blood-vessels (sinusoids); *Caps*, capsule of renal corpuscle; *Coel*, coelom; *col.T*, collecting tubule; *D*, dorsal; *Giz*, gizzard; *Glom*, glomerulus; *Gon*, gonad; *L*, left; *Spl*, spleen; *Sr.C*, cortical substance of suprarenal; *s.t*, secreting tubule; *T.R*, tubal ridge; *V*, ventral; *V.c.p*, posterior cardinal vein; *V.s'c.l*, left subcardinal vein; *W.D*, Wolffian duct.

often called the 'tubal ridge', Figs. 690-91. The groove forms a pit (sometimes two or three pits) which remains open in front and projects as a blind end into the fold behind (see further, p. 698). The opening becomes the ostium abdominale; the blind end gives rise to the duct itself by growing backwards independently between the outer 'tubal ridge' and the inner Wolffian duct, receiving contributions from neither of these structures (Braun, 1877-8; v. Milhalkovics, 1041, in Reptilia; Lillie, 845, and others, in *Gallus*; Fraser, 1010, in Marsupialia; Felix, 1005; Brambell, 994, and others, in Man and other Placentalia).

In the Amphibia also there extends back from the funnel area a band of specialised coelomic epithelium. According to Semon (1058-9) and Brauer (995) in Apoda the duct grows backwards from the funnel independently of both this band and the Wolffian duct. But according to some it may be derived anteriorly from the epithelium (MacBride, 1037, in *Rana*; Wilson, 1075, in Urodela), and according to others from the wall of the Wolffian duct (Gemmill, 1013, in Urodela; Hall, 1019, in Anura and Urodela). On the whole, the evidence seems to point to the Müllerian duct developing either independently, or possibly from the Wolffian duct at its posterior end only.

Scarcely less difficult to determine is the relation of the Müllerian funnel to the segmental tubules in Tetrapods. Clearly it is not merely an enlarged pronephric or mesonephric funnel; yet it seems generally to be related to the pronephric or anterior mesonephric tubules. Although Brauer (995) states that in the Apodan *Hypogeophis* the funnel area has no connexion with pronephric peritoneal funnels, it has been shown by H. Rabl in *Salamandra* (1049) and by Hall in Urodela and Anura that the Müllerian funnel is developed from an area at first continuous with the lips of one or more pronephric nephrocoelostomes. According to Hall's careful description of *Amblystoma*, patches of thickened coelomic epithelium extend ventrally in the pronephric chamber from two nephro-coelostomes; and a groove or funnel-like depression occurs in each patch. The patches join to a longitudinal funnel area, the blind ends of the pits grow back, fuse, and continue posteriorly as the rudiment of the duct. The funnel area passes forwards and downwards below the developing floor of the pronephric chamber, its edges close over, carrying the persisting opening of the posterior pit to its definitive position at the side of the liver. The ostium abdominale is thus originally derived from a patch of epithelium probably representing the remains of one or more pronephric peritoneal funnels. Although no such definite connexion with the pronephros has been described by recent observers in the Amniota except in the Crocodile (Wilson, 1074), yet the funnel area is usually situated very close to the vestigial pronephric or anterior mesonephric tubules. Certain structures in Mammals have been claimed by de Winiwarter (1076) and Wickmann to be remains of a connexion with the segmental tubules, and the latter describes pronephric funnels opening on the funnel area. Both in Birds and Mammals several depressions may occur on the surface of the area, and these may perhaps be interpreted as the last vestiges of peritoneal funnels; sometimes they give rise to accessory Müllerian funnels. Recently Brambell (994) has described the origin of the Müllerian funnel in the mouse from an invagination of the coelomic
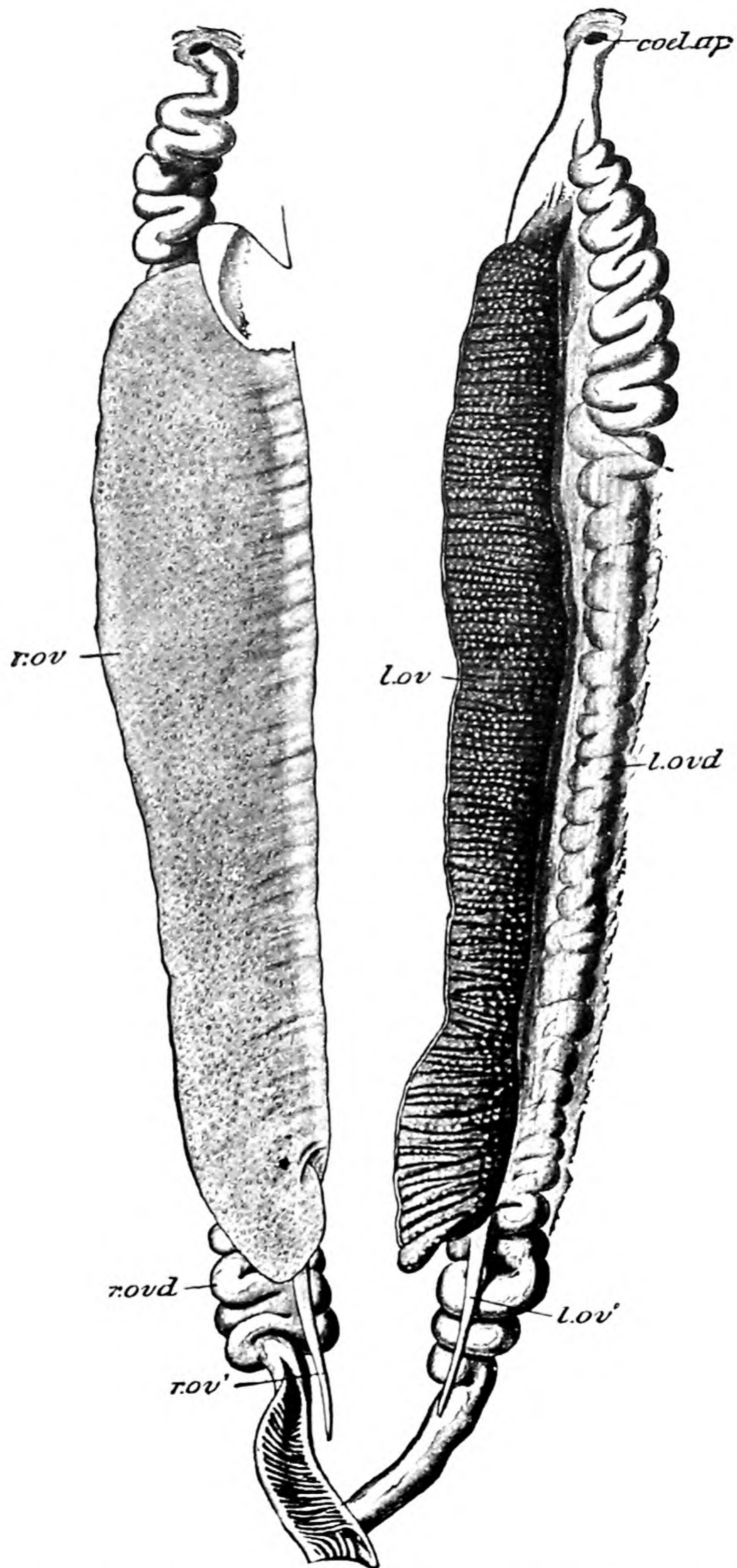
FIG. 692.

Ceratodus forsteri. Reproductive organs of female; the inner surface of the right and the outer surface of the left ovary shown. *coel.ap*, Coelomic aperture of oviduct; *l.ov*, left ovary; *l.ov'*, its posterior termination; *l.ovd*, left oviduct; *r.ov*, right ovary; *r.ov'*, its posterior termination; *r.ovd*, right oviduct. (After Günther, from Parker and Haswell, *Zoology*.)

epithelium in front of the mesonephros and occupying the same position on the urinogenital ridge as the peritoneal funnels further back.

The Dipnoi are provided with typical Müllerian ducts, which function as oviducts in the female. It is in this group that we might hope to find a clue to their morphology, but unfortunately they appear late, and their development is quite unknown, Fig. 692.

In Elasmobranchs the Müllerian ducts are both well developed and arise early in ontogeny, Figs. 684, 618-20. The funnels combine in the adult to a median ventral ostium situated behind the transverse septum and below the oesophagus and attachment of the liver. The ducts in the female acquire a large size, have a definite region specialised for secreting the egg-case, and open usually independently into the cloaca.[1] Although typical Müllerian ducts in function and anatomical relationships, they have been shown to develop from the pronephros and its duct (Semper, 1063; Balfour, 317). The funnel area is derived directly from the degenerate pronephric funnels, which combine to a single posterior opening (Balfour, Rabl, and others); it leads into the persisting last pronephric tubule and so to the longitudinal duct. The Müllerian duct itself develops by the gradual splitting off from before backwards of a second duct from the original primary duct. This progressive constriction of the primary duct into two gives rise to an upper true Wolffian duct and a lower Müllerian duct carrying the funnel at its anterior end. Posteriorly the two ducts come to open separately into the cloaca, Figs. 669, 670, 684.

Obviously, there is a striking difference between the development of the Müllerian ducts in Selachii and Tetrapoda; indeed, many have doubted its homology in the two groups. Yet so similar are the ducts in the adult condition both in function and in anatomical relationship that it can scarcely be doubted that they are homologous throughout the Gnathostomes (leaving the Teleostomes aside for the present; see below). Their constant presence in both sexes is a distinctive feature, and an important point is that in early stages the Müllerian funnel always occupies the same position—just behind the septum transversum and extending along the free edge of the anterior end of the nephric fold where it stretches down to the liver, Figs. 618-20, 625, 628, 649. Were it not for differences in its mode of development the homology of the Müllerian duct in Selachians and Tetrapods would scarcely have been questioned. But it is possible that these differences may be reconciled when its development becomes known in Holocephali and Dipnoi; and it is not

[1] Vestigial funnels remain in the male where the greater part of the duct is usually obliterated, but the posterior ends give rise to the 'seminal vesicles' (uterus masculinus).

impossible, even now, to devise a provisional reconciliation. Further knowledge of the development in other groups may enable us to solve this problem.[1]

Turning, now, to the conditions found in Teleostomes, the first fact that emerges is that in none of them have typical Müllerian funnels and ducts been found. This is one of the many features in their structure which exclude the Teleostomi from the direct line of ancestry of the Tetrapoda. When oviducts occur they are relatively short and their openings always somewhat far back, and, except in Acipenseridae, nothing resembling a Müllerian duct appears in the male, Fig. 682. Moreover, the oviduct extends along the outer side of the genital ridge close to its base,[2] instead of running along the outer side of the mesonephros, Fig. 683.

The Acipenseridae show, perhaps, the most primitive condition (Hyrtl, 1026). What appears to be a Müllerian duct is present in both sexes; in the female it is a wide tube lying close to the base of the elongated genital fold and opening about half-way up the ovary by a wide funnel. Posteriorly the oviduct opens into the urinogenital sinus leading to a median external pore. In the male a similar but smaller duct occurs in a corresponding position on the outer side of the genital fold; it has an anterior funnel and ends blindly in the wall of the urinogenital sinus.

[1] We have seen that in Tetrapods the funnel area is frequently connected with the pronephros, and may be derived from its peritoneal funnels; similarly in Selachians, since the pronephros is very degenerate and undergoes considerable remodelling at the time, it is possible that the funnel area also represents reduced pronephric peritoneal funnels. Even if the duct always develops by free backward growth in Tetrapods, it lies close to the latero-ventral side of the Wolffian duct—the splitting off, seen in Selachians, might have been omitted in the ontogeny of the Tetrapods, or on the contrary the continuity of the rudiments of the two ducts might have been secondarily established in the Selachian.

But another interpretation may prove to be nearer the truth. It is difficult to account for the presence of a 'tubal ridge' in Tetrapods if it has nothing to do with the development of the Müllerian duct, and it is possible that this duct may yet be shown to have arisen from the coelomic epithelium as a groove which became closed to form a tube opening behind into a mesonephric tubule and remained open in front. The peculiar mode of development of the duct in Selachians would then probably be secondary.

Since Müllerian duct and marginal canal often coexist in both sexes as separate structures they cannot be homologous, but the same objection does not apply with regard to the funnel area on which peritoneal funnels may open. It is not impossible that the funnel area may represent in front a special region of coelomic epithelium which further back becomes folded over to form the marginal canal (see further, p. 706).

[2] The statement frequently made in text-books that the oviduct lies on the inner or medial side of the genital fold in Teleostomes is erroneous. It extends between the genital and the nephric folds.

Very important is the condition seen in *Polypterus*, that isolated and in some respects primitive Actinopterygian (J. Müller, 1846; Hyrtl, 1026; Budgett, 10; Kerr, 1033). The oviduct of *Polypterus* has a wide opening about half-way up the ovary and passes back beyond it to open into the urinogenital sinus (near the place where the two mesonephric ducts join to a median sinus probably derived from a cloaca). The sinus opens on a urinogenital papilla behind the anus. *Amia* has very similar oviducts, which join and open between the anus in front and the urinary pore behind, Figs. 683, 693.

Lepidosteus presents a new type of structure in the female (Balfour and Parker, 2) since each ovary projects into a closed sac continuous with a duct behind, which opens into the base of the mesonephric duct. The two mesonephric ducts join to a sinus opening to the exterior by a median pore. In this fish, then, the ripe ova are carried out directly, and are not first shed into the general coelom, Figs. 683, 693.
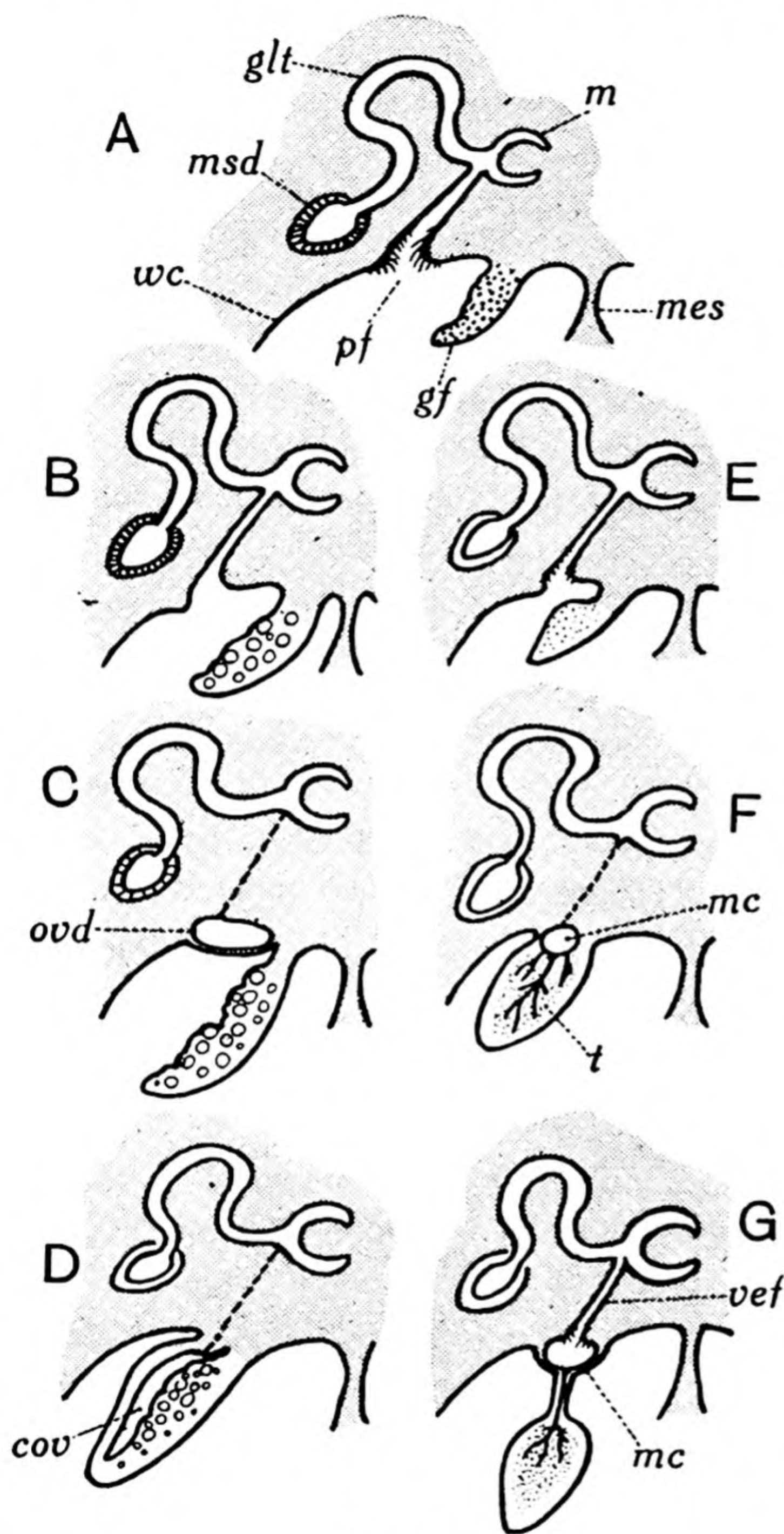
FIG. 693.

Diagrams illustrating relation of *genital fold* and *mesonephric tubule* to oviduct on left and to marginal canal of testis on right in *Teleostomes*. A, Primitive indifferent condition; B, *Polypterus* ♀, young stage; C, *Polypterus* ♀, adult; D, *Lepidosteus* ♀, adult; E, *Polypterus* ♂, young stage; F, *Polypterus* ♂, adult; G, *Lepidosteus* ♂, adult. *cov*, Cavity of ovary; *gf*, genital fold; *glt*, glandular tube; *m*, capsule of Malpighian body; *mc*, marginal canal; *mes*, mesentery; *msd*, mesonephric duct; *ovd*, oviduct = marginal canal; *pf*, peritoneal funnel; *t*, testis; *vef*, vas efferens (funnel canal); *wc*, wall of splanchnocoele.

The Teleostei present various interesting types of structure in the

female, some approaching that seen in *Amia* and others that seen in *Lepidosteus* (Rathke, 1820–25; Hyrtl, 1025). The morphology of the Teleostean ducts is very difficult to interpret, and the homology of the
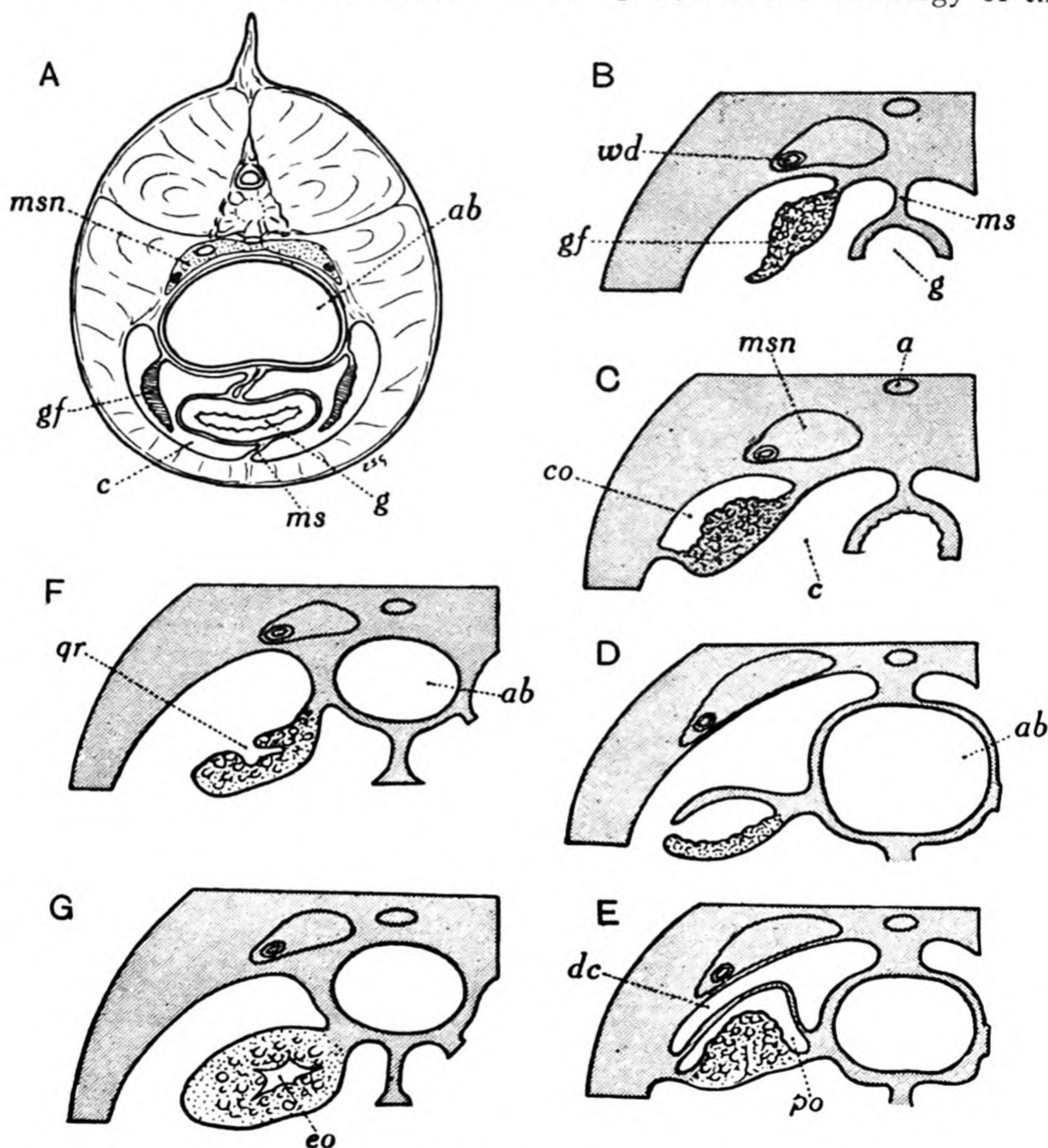
FIG. 694.

A, Transverse section of *Anguilla vulgaris*, showing free ovaries hanging in coelom. B-G, Diagrammatic sections showing development of closed ovaries. B and C, *Cobitis*; early stage with genital fold free, and later stage with fold fused to coelomic wall (after Schneider, 1895). D and E, *Cyprinus*; early stage with ovary still open, and later stage with fold fused and cavity closed (after Haller, 1905). F and G, *Acerina*; early stage free and open, and late stage closed (after Jungersen, 1889). *ab*, Airbladder; *c*, splanchnocoele; *co*, ovarian cavity cut off from coelom; *dc*, dorsal coelomic chamber; *eo*, endovarial cavity; *g*, gut; *gf*, genital fold; *ms*, mesentery; *msn*, mesonephros; *po*, parovarial cavity; *qr*, parovarial groove; *wd*, mesonephric duct.

parts by no means yet established. A few Teleosts have so-called 'free ovaries', which shed the ova into the general coelom in the usual manner. In such forms the ova may be carried to the exterior by oviducts resem-

bling those of *Amia* or may pass out by mere pores. *Osmerus*, among the Salmonidae, has oviducts almost as well developed as those of *Amia*; but in *Salmo* they are reduced to short funnels behind the ovary and leading to the median pore, while *Mallotus, Coregonus*, and *Argentina* show intermediate stages (Huxley, 1024 ; Weber, 1069). The Galaxiidae, Notopteridae, Hyodontidae, Osteoglossidae, and the Cyprinid *Misgurnus*, have similar free ovaries and very short oviducts. Finally, in Anguilli-formes the ova when shed into the coelom pass out directly by a median pore, Figs. 683, 694-7.

But in the majority of Teleostei, including all the highest families, there are ' closed ovaries ' or ovisacs. In these the ripe ova fall into
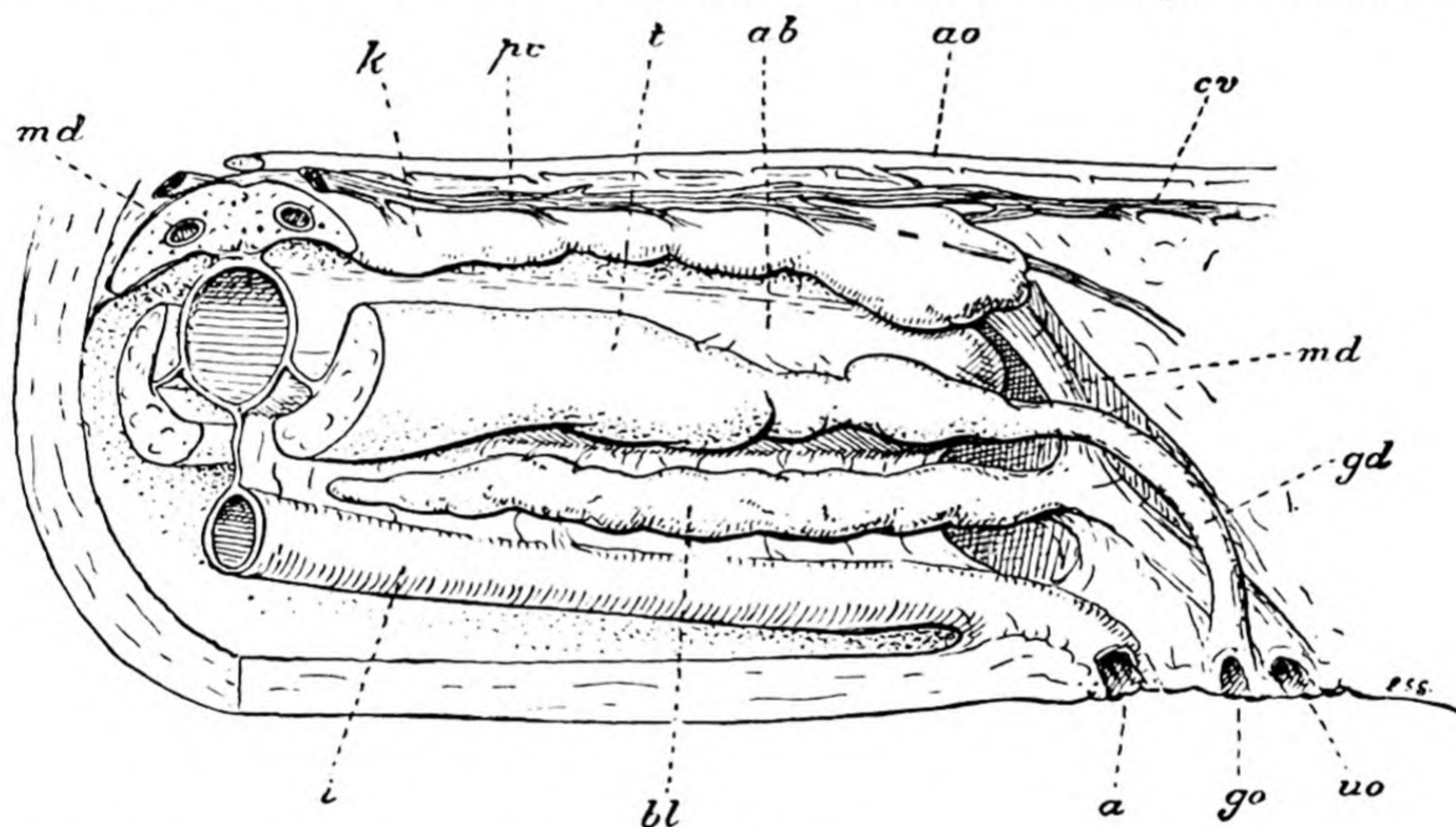
FIG. 695.

Left-side view of a dissection of a male *Esox lucius*, L., showing the median apertures of the rectum, genital ducts, and kidney ducts. *a*, Anus ; *ab*, air-bladder, blind hinder end ; *ao*, dorsal aorta ; *bl*, urinary bladder ; *cv, gd*, vas deferens ; *go*, genital opening ; *i*, intestine ; *k*, kidney (mesonephros) ; *md*, mesonephric duct ; *pc*, posterior cardinal ; *t*, testis ; *uo*, urinary opening. (From Goodrich, *Vert. Craniata*, 1909.)

an ovarian cavity having no communication with the general body-cavity ; the two ovarian sacs narrow behind to form oviducts which usually combine to open by a median pore between anus and urinary pore. This genital pore, situated behind the anus and in front of the urinary pore, is doubtless homologous throughout the Teleosts (see further, p. 710).

Several questions arise in connexion with the female organs of the Teleostei : Which is the primitive condition, the free ovary or the ovarian sac ? the long oviduct of *Osmerus* or the pore of *Anguilla* ? Are the oviducts homologous with Müllerian ducts or with the longitudinal marginal canal occupying much the same position in the male of primitive Teleostomes ?

The cavity of the ovarian sac may be distinguished into two parts : the first or ovarial part related to the ovary itself, and the second part forming the lumen of the duct leading to the pore, Figs. 694, 696-7. While in such a form as *Anguilla* the genital fold remains as a simple band on the outer side of which the ova develop, in others a chamber is formed by the grooving of this ovarian surface, or the folding of the band on itself, or the fusion of its free edge with the coelomic wall (Macleod, 1038; Jungersen, 1028 ; Schneider, 1052 ; Haller, 1020). When the edge of the genital fold bends outwards and fuses with the outer wall of the coelom (*Rhodeus, Gobio, Esox,* etc.), or bends up to fuse close to its attachment, the chamber lies at the side of the ovary, and is called a parovarial canal. An endovarial canal occurs when the outer surface of the band becomes grooved and the two edges of the groove meet and fuse (*Acerina, Perca,* etc.). There is no fundamental distinction between the two types, and in *Salmo* the front end of the ovary is folded so as to
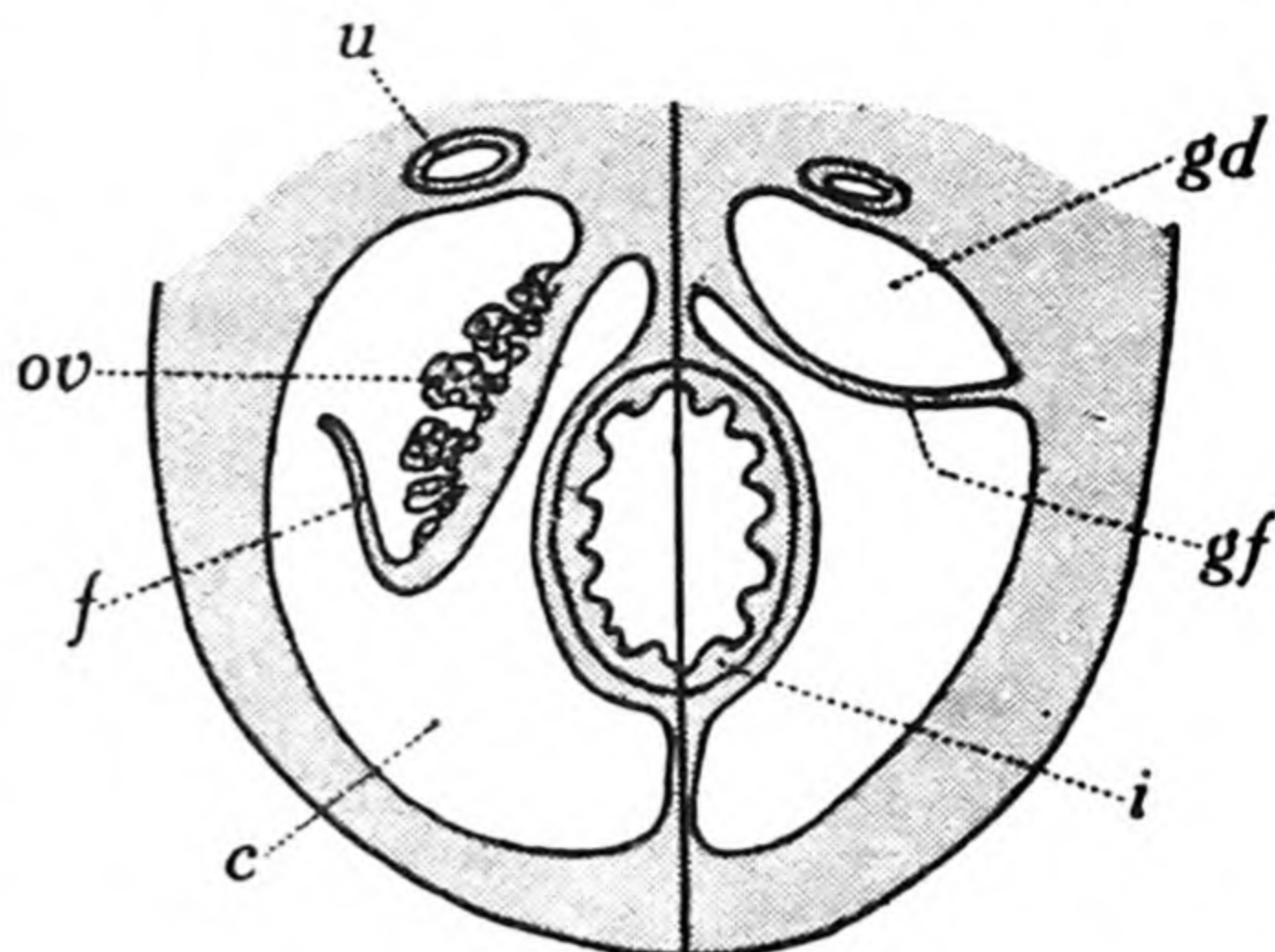
FIG. 696.

Diagrammatic transverse sections of a Teleost; on left through ovary, *ov*, on right more posteriorly through genital duct, *gd*. *c*, Splanchnocoele; *f*, free edge of genital fold; *gf*, genital fold forming behind ventral wall of duct; *i*, intestine; *u*, ureter (mesonephric duct).
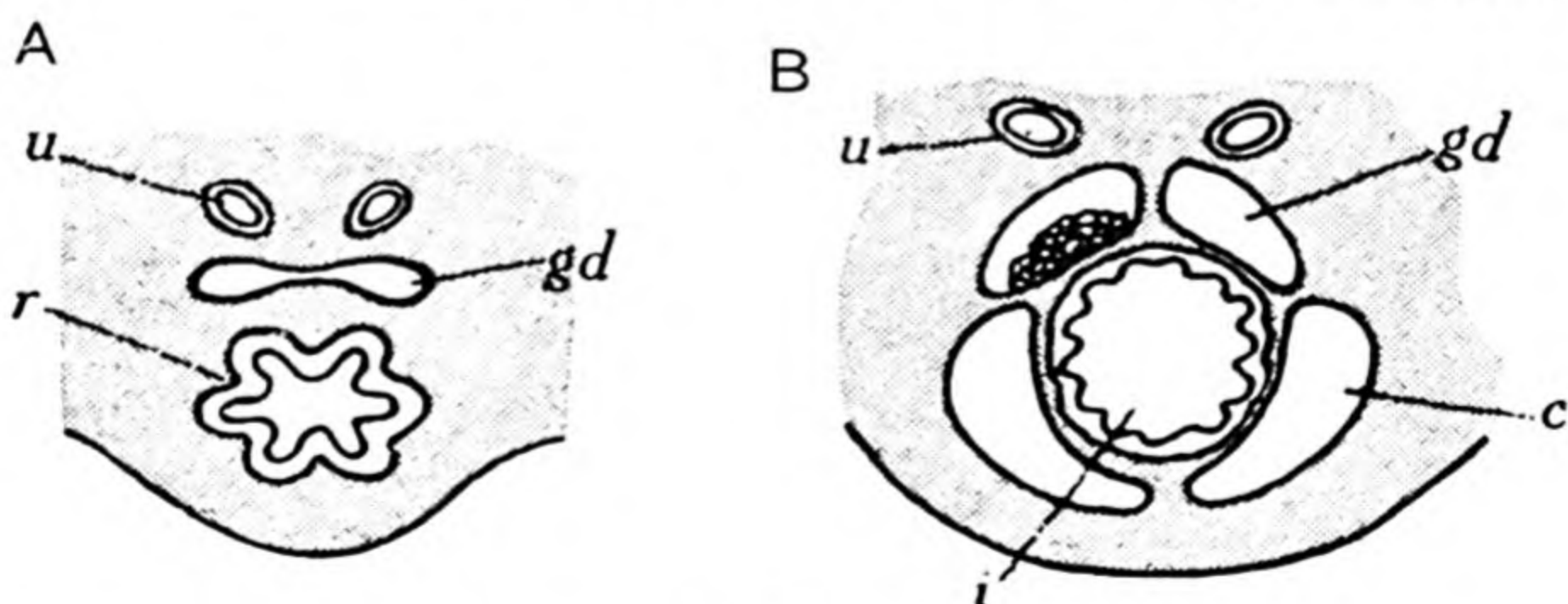
FIG. 697.

Diagrammatic transverse sections showing genital duct and coelom in ♀ *Teleost* : A, More posterior section just in front of anus ; B, section through hinder region of trunk coelom, *c*. *gd*, Oviduct or dorsal chamber of coelom containing hind end of ovary on left ; *i*, intestine ; *r*, rectum ; *u*, mesonephric duct.

form a short parovarial canal, while a short endovarial canal is developed behind, both remaining open (Felix u. Bühler, 1007). All Teleosts pass through a stage with free ovary. Clearly the closed sac is derived from a more primitive simple band-like genital fold. In answer to the question

whether the ancestral Teleosts had free or closed ovaries, we have the view of Brock that the free ovary seen in *Anguilla* is primary, and that of Balfour that it is more probably secondary due to a return to an apparently primitive condition from the closed structure already established in *Lepidosteus*. The sporadic occurrence of the ' free ' condition in various unrelated Teleostean families is strong evidence in favour of Balfour's suggestion.

As to the homology of the Teleostean oviducts and genital pores the evidence is still uncertain. Waldeyer held that the duct is a reduced Müllerian duct, and that in forms with closed ovarian sacs the ovaries have been overgrown and enclosed by the Müllerian funnel (**1067**). Balfour suggested that in *Lepidosteus* the closed sac has probably been formed by the junction of an ovarian chamber of the coelom (parovarial canal) with a posterior short Müllerian duct opening into it (**2**). The ' free ' ovary in Teleosts would, then, be due to the failure of these two structures to unite. On the whole this suggestion agrees best with the facts. Jungersen (**1028**) has shown that the duct proper may develop by the hollowing out of a thickening of the coelomic epithelium before (*Acerina*) or after the formation of the ovarian cavity (*Esox*, *Zoarces*, etc.), and recently Essenberg has described the separate origin of the posterior duct and the parovarial canal in *Xiphophorus* (**1004**).

On the other hand, Brock (**998-9**), Felix (**1007**), and Lickteig (**1035**) maintain that the Teleostean oviduct is not a Müllerian duct, but merely a prolongation backward of the paired dorsal regions of the coelom (ovarian sacs in forms with closed ovaries) which join and open by a common pore to the exterior. Such a view necessitates the assumption that the Müllerian ducts and their primitive openings have disappeared altogether, and been replaced by new formations. Considering how universally Müllerian ducts occur in other groups, it seems more reasonable to suppose that the oviducts of Teleostomes are, at all events in part, homologous with them,[1] and that their original openings have persisted in phylogeny and are represented in Teleostei by the genital pore (pp. 704, 711).

Obscure as is the origin of the Müllerian duct in Gnathostomes generally, the oviduct of Teleostomes can scarcely be its complete homologue. For the researches of Balfour and Parker on *Lepidosteus* (**2**), of Budgett (**10**) and Kerr (**1033**) on *Polypterus* (and apparently of Maschkovzeff on

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[1] It should not be forgotten that the oviducts in Acipenseridae are represented in the male (p. 701), and it is not impossible that vestiges of Müllerian ducts may yet be discovered in other Teleostomes where they appear to be absent when their structure and development come to be better known.

Acipenser (1040)), clearly prove that whereas the duct posterior to the ovary may represent a Müllerian duct, the more anterior part alongside the ovary is of different nature. This latter part is a longitudinal chamber of the coelom closed off at the base of the genital folds; into it, at first, open the mesonephric peritoneal funnels, Fig. 693. This canal in the female has in fact much the same relations as the marginal canal in male Gnathostomes generally (see also female, p. 694). Felix, indeed, compares the whole oviduct of Teleostomes to a marginal canal; but it would seem more probable that in these fish a short Müllerian duct has been prolonged by the closing over of a canal, carrying the ostium abdominale forward. This would give rise to the elongated oviducts seen in *Amia* or *Polypterus*; by reduction from in front the condition seen in Salmonids and lastly in Eels would be brought about. The widening of the canal so as to enclose the whole of the fertile region of the genital fold and closure of the ostium might give rise to the ovarian sac of *Lepidosteus* and Teleostei.

THE GENITAL DUCTS OF THE CYCLOSTOMATA

There remain to be considered the genital pores or funnels of the Lampreys and Hag-fishes. It has already been mentioned that the Cyclostomes differ from the Gnathostomes in that their genital products do not pass out through the segmental tubules in the male. The gonads are built on the same general plan, and develop from paired genital folds; but in both sexes the ripe germ-cells are shed into the general coelom and escape to the exterior through genital pores of paired origin. Thus, not only are there no vasa efferentia, but also no Müllerian ducts; unless, indeed, these pores represent them. In the Petromyzontia the pores open on either side into a urinogenital sinus provided with a median pore on a papilla situated behind the anus, Fig. 98. This sinus appears to be formed by the subdivision of an original endodermal cloaca into which open the primary archinephric ducts in the larva. The cloaca in the Myxinoidea is less completely divided, and the two genital pores here unite to open into it just behind the anus and in front of the urinary pore, Fig. 100.

The morphological significance of these genital pores is difficult to determine. It has been claimed that they are mere 'abdominal pores' (Lickteig, 1035); but their anatomical relations do not support this view. The possibility that they represent a posterior pair of segmental tubules (coelomoducts), which have retained their original function of conveying the genital products to the exterior, must be kept in mind.

THE URINARY AND GENITAL PORES, AND THE CLOACA

Before leaving the subject of the excretory system of the Craniata something must be said about the external pores of the ducts, and the development and fate of the cloaca. A cloaca into which open rectum, urinary, and genital ducts is found in primitive Craniates. That of the Cyclostomes has been described above. All primitive Gnathostomes retain a cloaca (Selachii, Fig. 684, Dipnoi, Figs. 682-3, Amphibia, Reptilia,
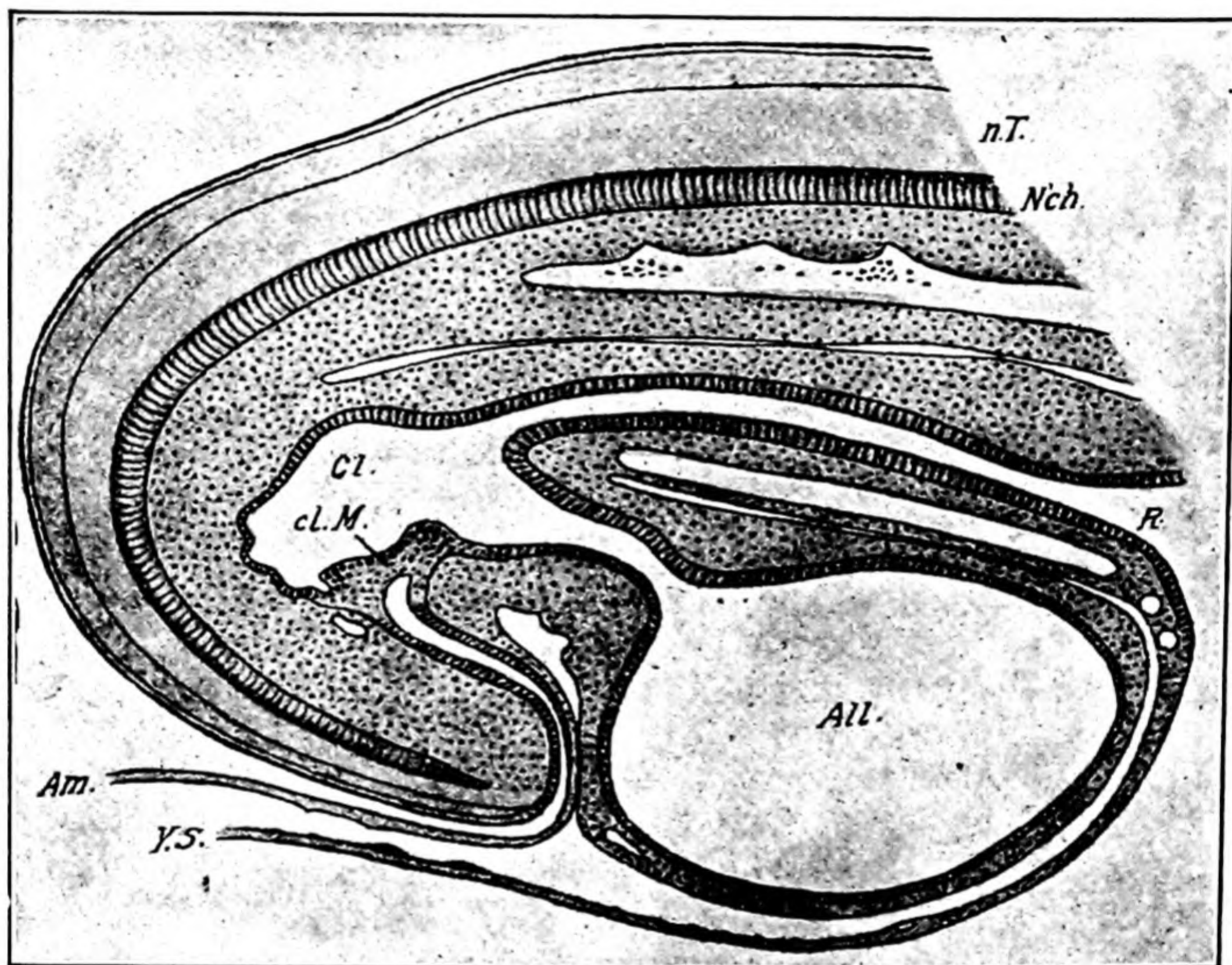
FIG. 698.

Median sagittal section of hind end of chick embryo on fourth day of incubation (after Gasser, from F. R. Lillie, *Develt. Chick*, 1919). *All*, Allantois ; *Am*, tail fold of amnion ; *cl.M*, cloacal membrane ; *Cl*, cloaca ; *N'ch*, notochord ; *n.T*, neural tube ; *R*, rectum ; *Y.S*, wall of yolk-sac.

Fig. 700, Aves, Fig. 701, Monotremata); but it is more or less completely lost in specialised groups (Holocephali, Fig. 167 c, Teleostomi, Figs. 682-3, 695, Mammalia Ditremata, Fig. 702). In the Gnathostomes the cloaca is formed partly from the endodermal gut and partly from an ectodermal invagination or proctodaeum. Endoderm and ectoderm coming into contact form a cloacal plate or membrane ; the primitive anus arises by the breaking through of this membrane generally late in embryonic life.[1]

[1] It is frequently held that the primitive anus in Vertebrates has been derived from the blastopore ; but the interpretation of its development has been much influenced by theories of more than doubtful value. Certainly in

Into the embryonic cloaca lined by endoderm come to open the primary archinephric and later the Müllerian ducts, while the posterior region of the cloaca lined by ectoderm opens to the exterior by the median cloacal aperture. The share taken by the endoderm and ectoderm in the formation of the definitive cloaca varies considerably in different groups.
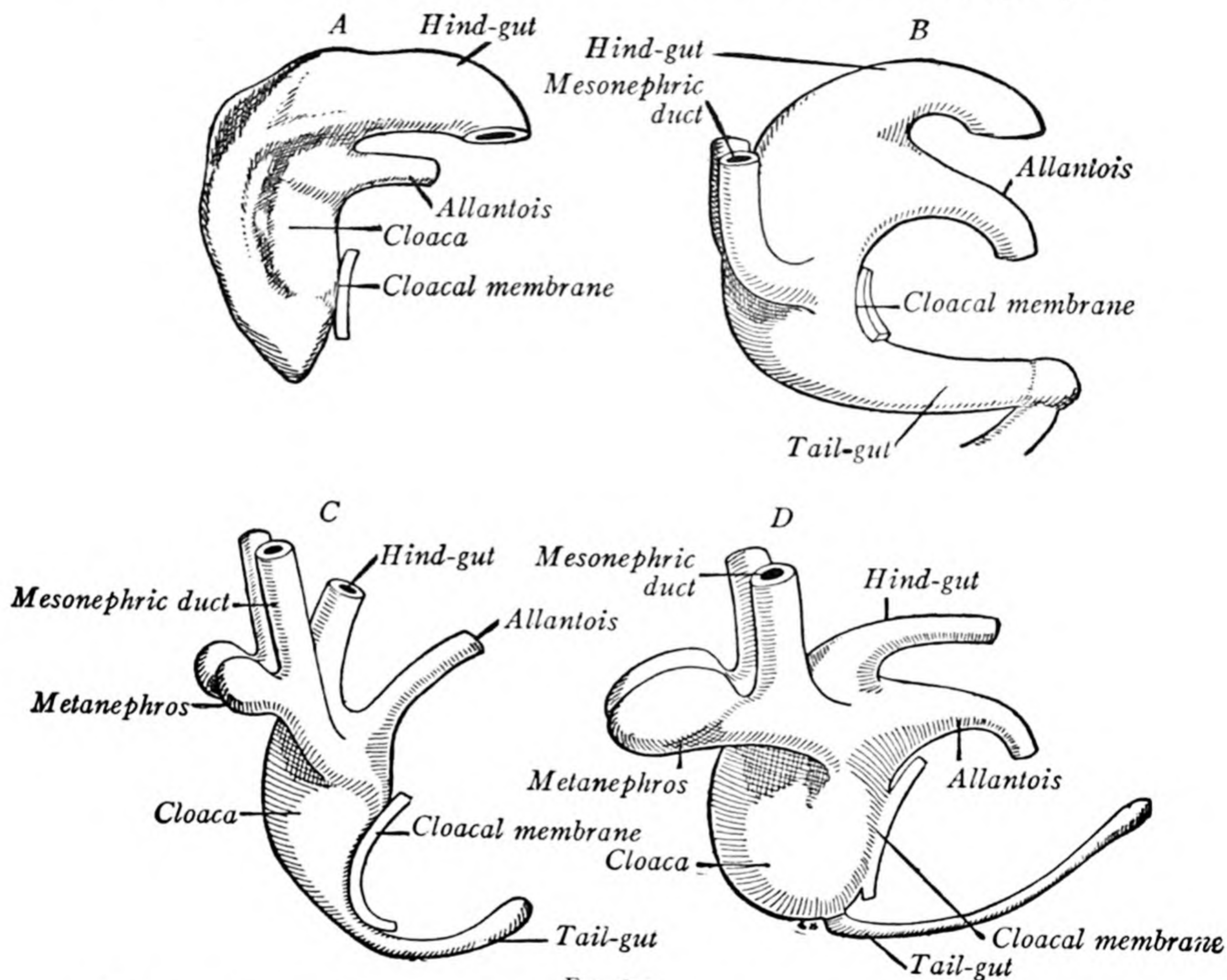
FIG. 699.

Four stages showing differentiation of cloaca into rectum, urethra, and bladder (after reconstructions by Pohlman). ×about 50. A, Human embryo, 3·5 mm.; B, about 4 mm.; C, 5 mm.; D, 7 mm. (From Prentiss and Arey, *Text-book of Embryology*, 1917.)

The cloaca of adult Selachians is shallow and widely open. Into it open the rectum, the mesonephric ducts (urinary sinus) at the end of a dorsal papilla, and the Müllerian ducts. The cloaca of the Holocephali is so shallow as to be lost, and the rectum and ducts come to open separately

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Amphioxus the blastopore becomes the opening into the neurenteric canal, and has nothing to do with the anus which appears independently and later. The same is probably true of all vertebrates. Although in some animals, such as the Frog, the two apertures may appear closely related, it is difficult to see how this can be anything but secondary. The case of *Petromyzon*, in which the blastopore is said to persist as the anus, needs impartial reinvestigation.

to the exterior. The Dipnoi retain a primitive cloaca, and from the base of the united mesonephric ducts arises a bladder-like caecum lying dorsally to the rectum. On the other hand, the Teleostomi have lost the cloaca owing to its subdivision into ventral, rectal, and dorsal urinogenital portions. In the lower forms, such as *Polypterus, Acipenser, Lepidosteus,* and *Amia,* there is a urinogenital sinus opening by a median pore behind the anus; but in Teleosts this sinus is usually subdivided, so that a separate median genital pore occurs between the anus and urinary pore. Occasionally, however, the sperm-ducts open into the base of the mesonephric ducts (Anguilliformes, *Anablebs, Perca, Zoarces, Cyclopterus,* etc.), or together with the anus (*Lota*), or with both the anus and the kidney as in Lophobranchii (Hyrtl, 1025; Stannius, 1854–6). A median mesodermal bladder-like diverticulum is often developed from the united bases of the mesonephric ducts which contribute to the formation of the urinogenital sinus, Fig. 695.

A typical cloaca is found in Amphibia, and from its mid-ventral endodermal wall is developed the true urinary bladder characteristic of the Tetrapoda. A similar cloaca

FIG. 700.

Female urinogenital apparatus of *Lacerta muralis.*
B, Urinary bladder; *B¹,* neck of the bladder (cut open); *N,* kidneys; *Od,* oviducts, which open into the cloaca at *Od¹*; *Ot,* abdominal openings of oviducts; *Ov,* ovaries; *R,* rectum; *R¹,* opening of rectum into the cloaca (*Cl*); *Ur¹,* apertures of the ureters into the cloaca; †, remains of mesonephros. (From Wiedersheim, *Comp. Anatomy.*)

occurs in Reptiles and Birds, but here its ectodermal ventral wall becomes strengthened by an upper corpus spongiosum and
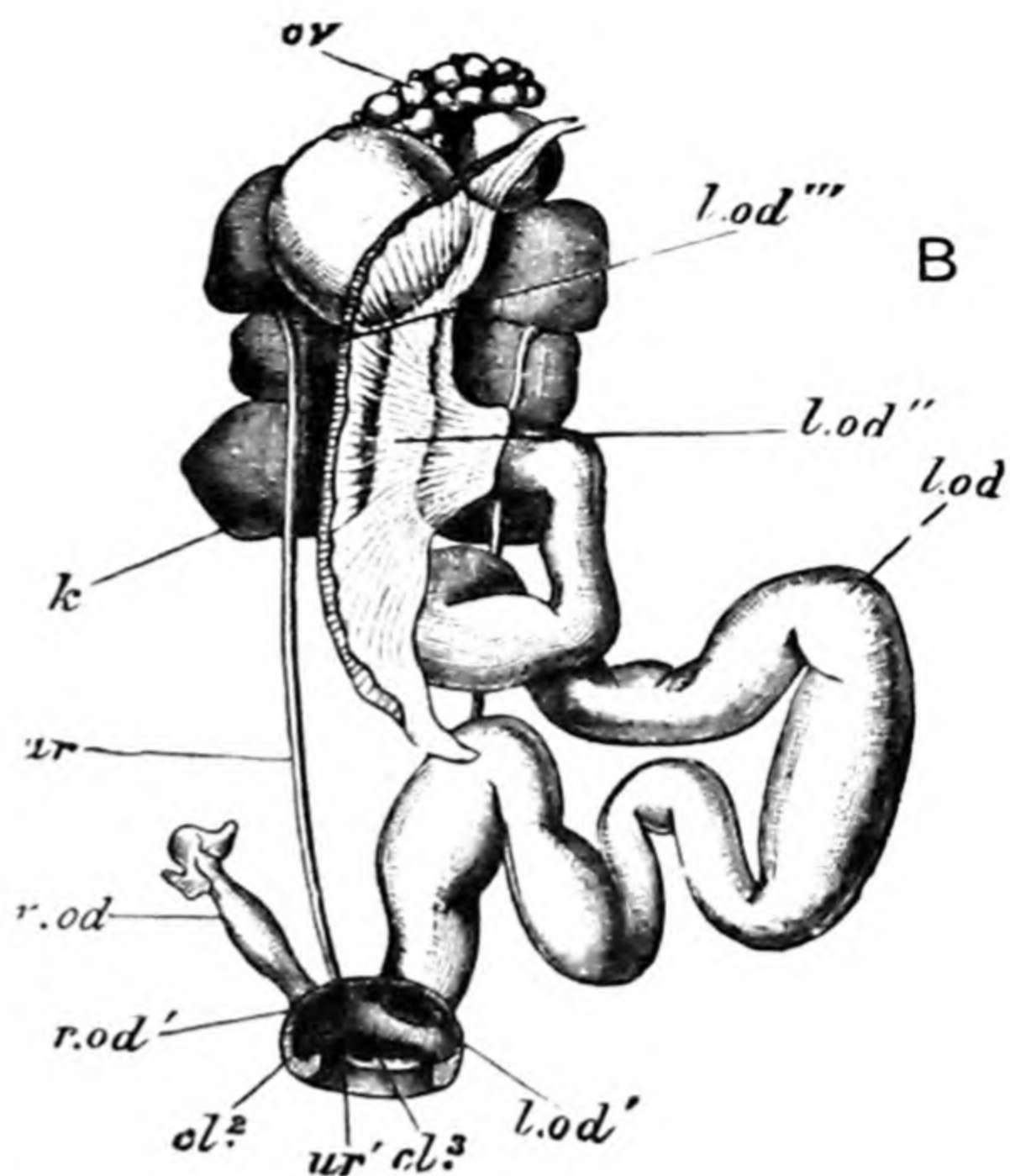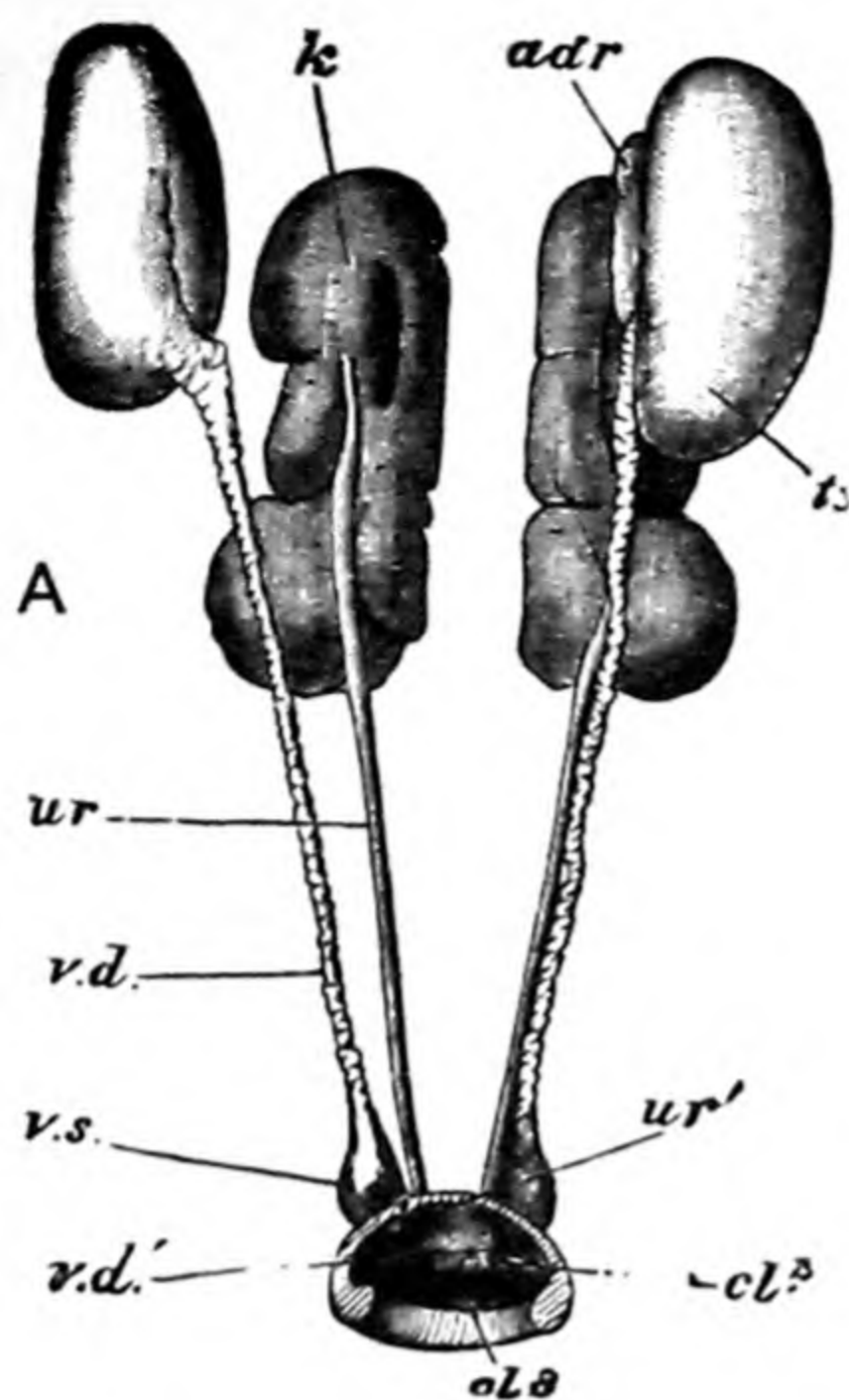
FIG. 701.

Columba livia. A, Male urinogenital organs. *adr*, Adrenal; *cl.* 2, urodaeum; *cl.* 3, proctodaeum; *k*, kidney; *ts*, testis, that of the right side displaced; *ur*, ureter; *ur'*, aperture of ureter; *v.d*, vas deferens; *v.d'*, its cloacal aperture; *v.s*, vesicula seminalis. B, Female urinogenital organs. *cl.* 2, Urodaeum; *cl.* 3, proctodaeum; *k*, kidney; *l.od*, left oviduct; *l.od'*, its cloacal aperture; *l.od"*, its coelomic funnel; *l.od"'*, its coelomic aperture; *ov*, ovary; *r.od*, right oviduct; *r.od'*, its cloacal aperture; *ur*, ureter; *ur'*, its cloacal aperture. (From Parker's *Zootomy*.)
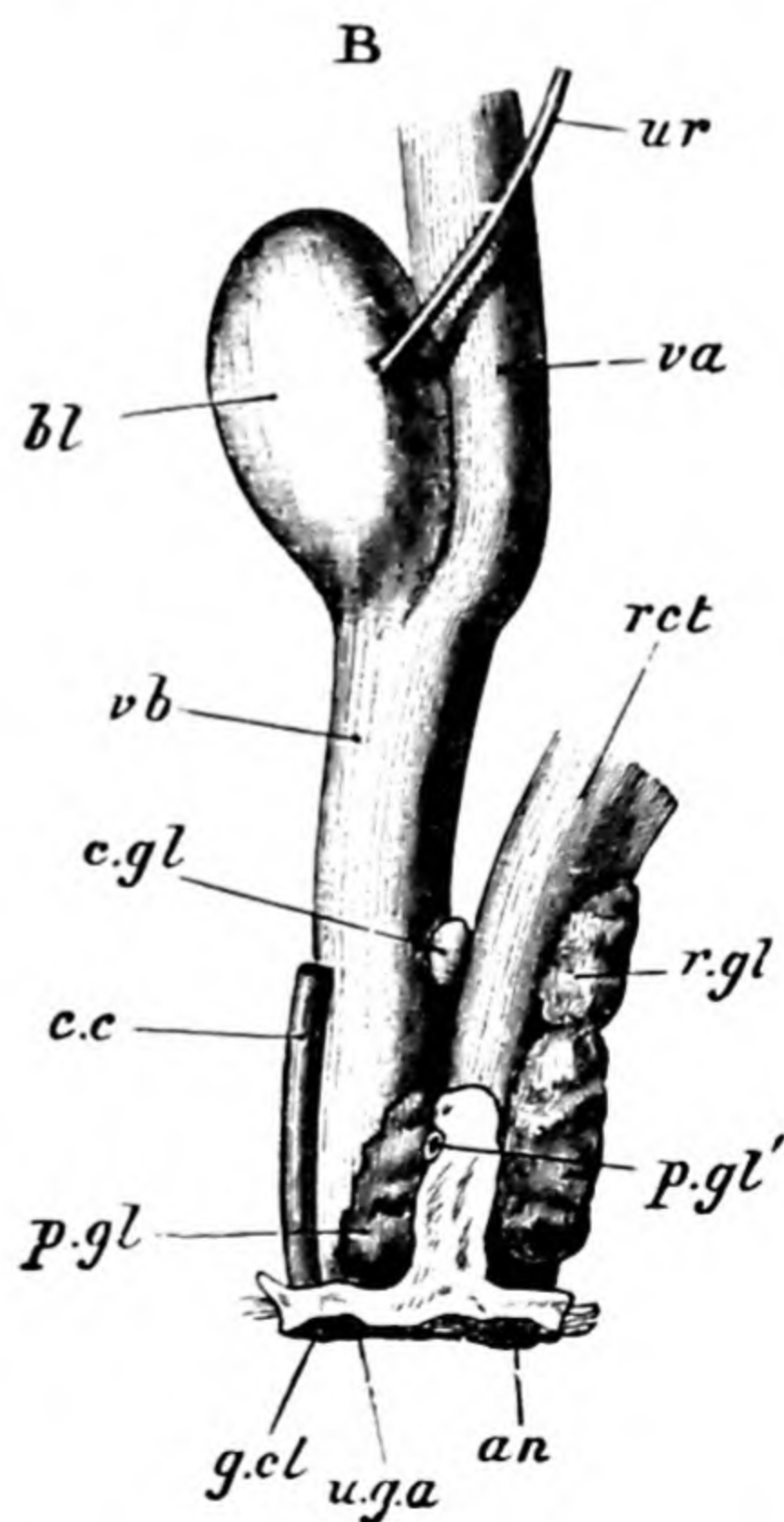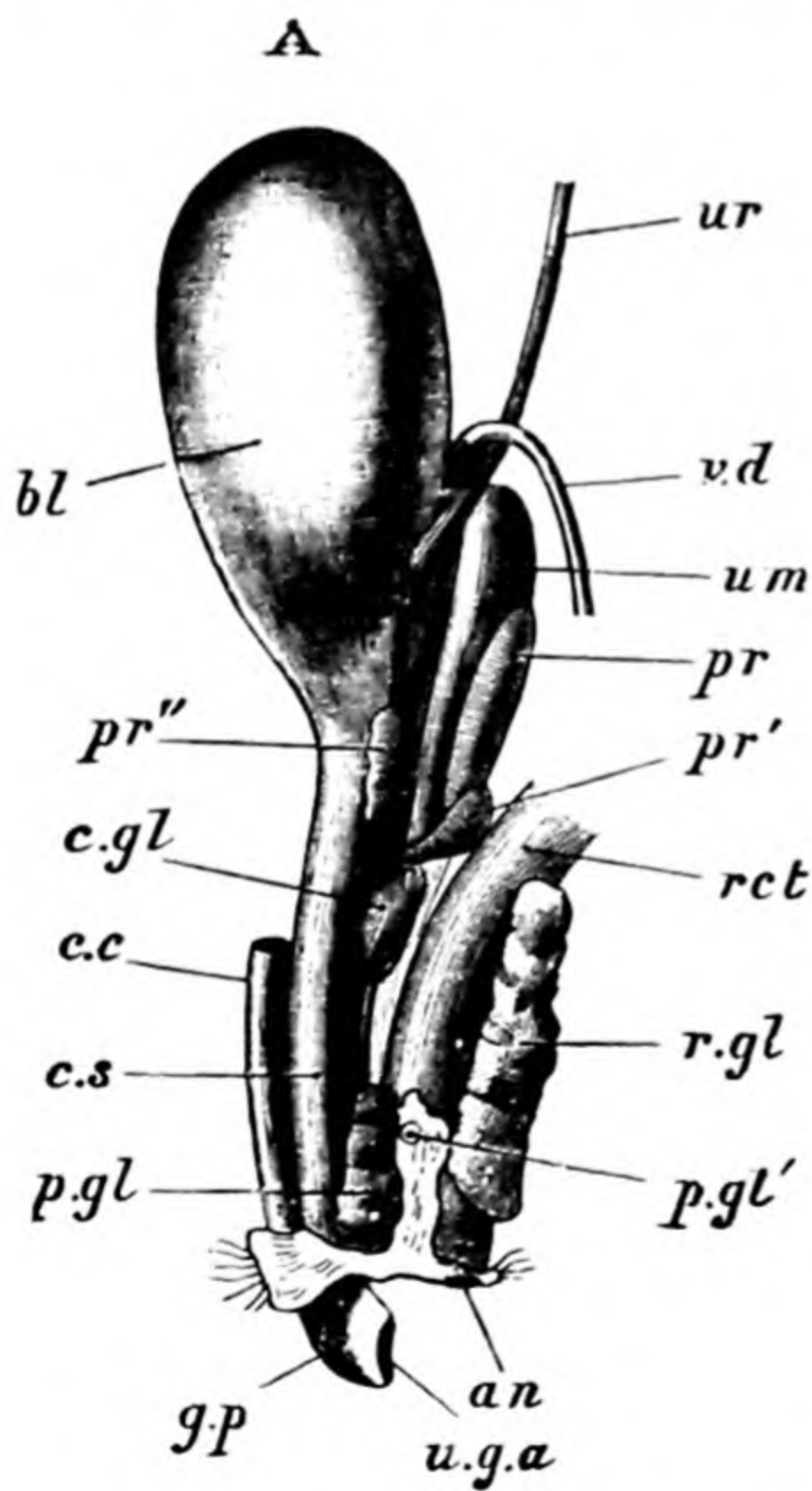
FIG. 702.

Lepus cuniculus. The urinogenital organs; A, of male; B, of female; from the left side (half nat. size). The kidneys and proximal ends of the ureters, in A the testes, and in B the ovaries, Fallopian tubes and uteri are not shown. *an*, Anus; *bl*, urinary bladder; *c.c*, corpus cavernosum; *c.s*, corpus spongiosum; *c.gl*, Cowper's gland; *g.cl*, apex of clitoris; *g.p*, apex of penis; *p.gl*, perineal gland; *p.gl'*, aperture of its duct on the perineal space; *pr*, anterior, *pr'*, posterior, and *pr"*, lateral lobes of prostate; *rct*, rectum; *r.gl*, rectal gland; *u.g.a*, urinogenital aperture; *u.m*, uterus masculinus; *ur*, ureter; *va*, vagina; *vb*, vestibule; *v.d*, vas deferens. (From Parker's *Zootomy*.)

a lower corpus fibrosum, which become converted into the copulatory organ of the male (Fleischmann, A., 1009; Pomayer, 1046; v.
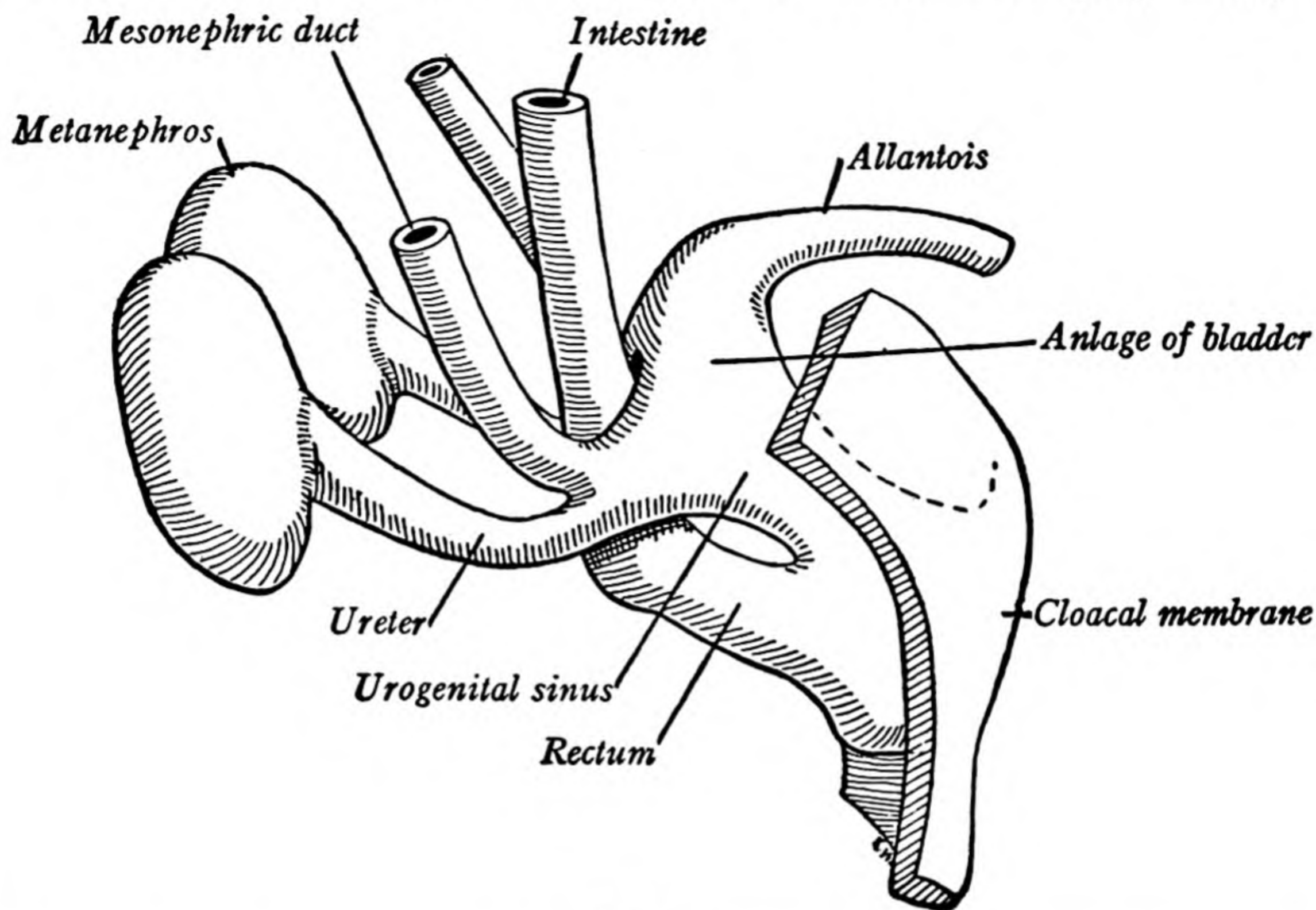
FIG. 703.

Reconstruction from 12 mm. human embryo showing partial subdivision of cloaca into rectum and urinogenital sinus (after Pohlman). × 65. (From Prentiss and Arey, *Text-book of Embryology*, 1917.)
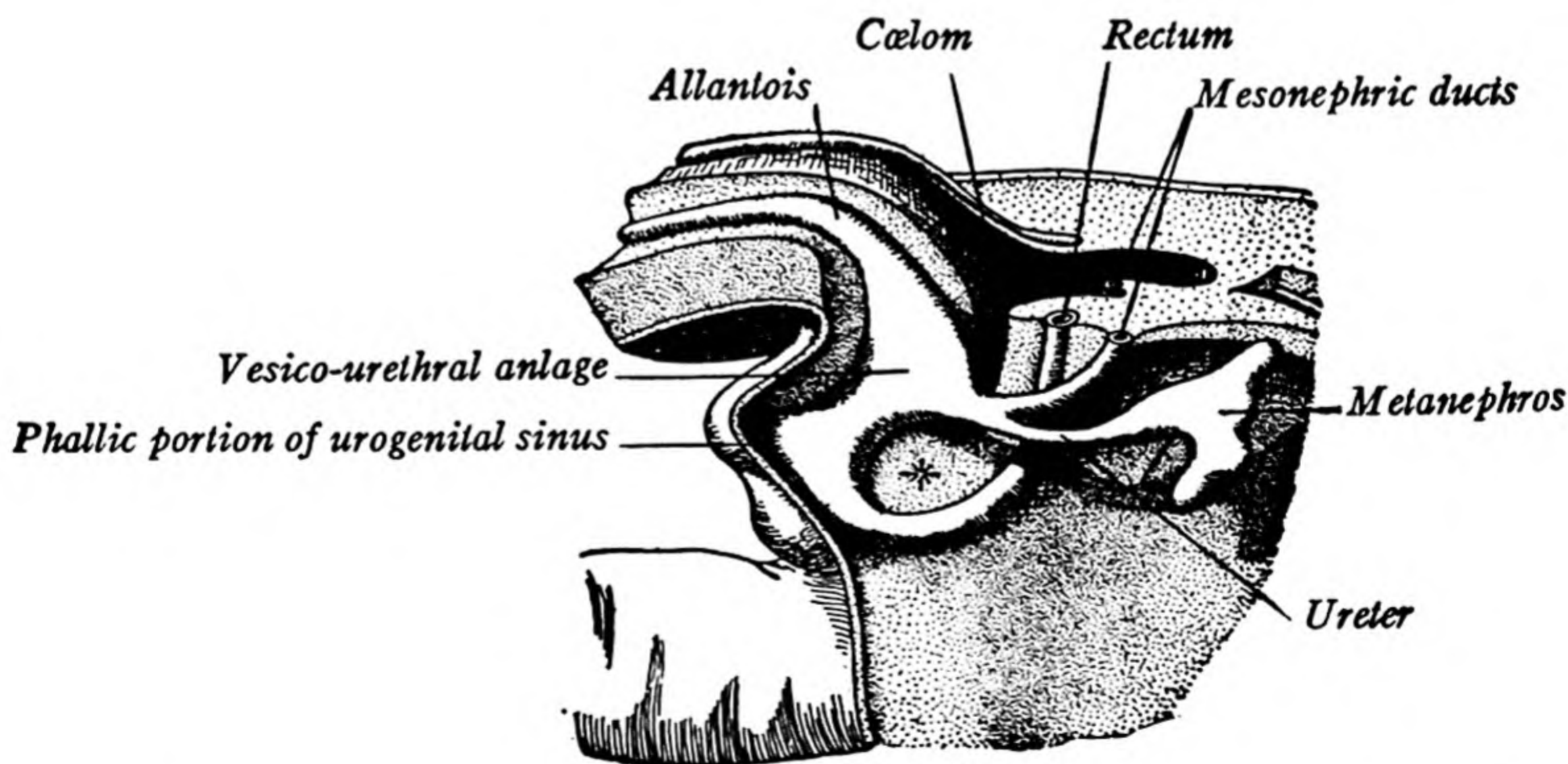
FIG. 704.

Reconstruction of caudal portion of 11·5 mm. human embryo showing differentiation of rectum, bladder, and urethra (after Keibel's model). × 25. (From Prentiss and Arey, *Text-book of Embryology*, 1917.)

Oordt, 1922; Boyden, 992; Hellmuth, 1021). The ventral endodermal diverticulum is enlarged to give rise in the embryo to the allantoic

sac characteristic of the Amniota, and the adult bladder is formed from its enlarged base only,[1] Figs. 698-9. In the Mammalia the cloaca tends to disappear as such in the adult (Gerhardt, 1014-1015; Brock, 997). Its endodermal region becomes subdivided by a backwardly growing fold into an upper or postero-dorsal rectum, and a lower or antero-ventral urinogenital canal into which open the bladder, ureters, and genital ducts. Its ectodermal region also becomes subdivided in the male. For, while in Reptiles the spermatozoa pass along open grooves on the copulatory organ, in the Mammal the median groove
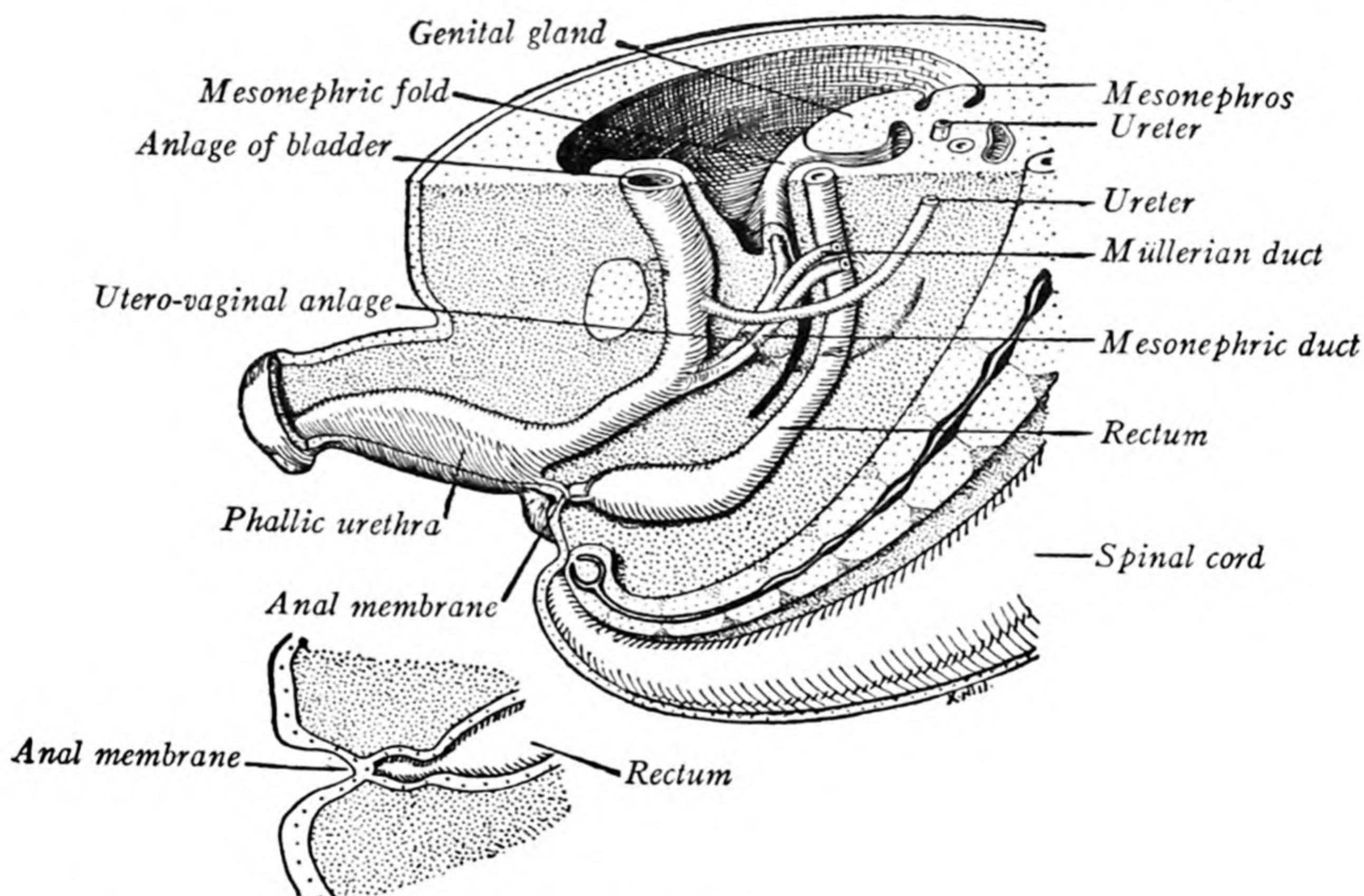
FIG. 705.

Reconstruction of caudal end of 29 mm. human embryo showing complete separation of rectum and urinogenital sinus and relations of urinogenital ducts (after Keibel's model). × 15. (From Prentiss and Arey, *Text-book of Embryology*, 1917.)

becomes closed over to form a tube, the penial urethra (phallic urethra). The very primitive character of these structures in Monotremes is shown in the persistence of the compound cloaca, and its single opening, and the incomplete closure of the urethra anteriorly, so that the urinogenital

[1] In Birds there is a considerable ectodermal cloaca into which comes to open a median dorsal bursa Fabricii, developed from the wall of the endodermal cloaca. It usually atrophies in the adult and its function is doubtful; but it may produce an internal secretion at the onset of sexual maturity (Wenckebach, 1888; Pomayer, 1046; Boyden, 992). Dorsal paired lateral bladder-like pouches are developed in some Reptiles (Chelonia).

canal still remains in communication with the dorsal cloacal chamber by a narrow 'urinary canal' (Keibel, **1030**). In the Ditremata, on the other hand, the fold separating the rectal from the urinogenital chambers extends as far as the cloacal membrane, so that the anus and urinogenital apertures come to open separately (Keibel, **1030** ; Felix, **1006** ; Brock, **997**). At the same time on the phallic thickening anterior to the latter is formed a groove which closes to a urethral canal in the male carrying the urinogenital opening to the extremity of the penis. The urinary canal (communication between the urinogenital and rectal chambers) is closed in the Ditremata (except in *Perameles* according to v. d. Brock), Figs. 703-5.

In the Marsupialia the anus and urinogenital aperture lead into a considerable shallow ectodermal cloaca the opening of which is closed by a sphincter muscle. A small ectodermal cloacal region may occur in some of the lower Placentalia (some Rodents and Insectivores), but in the majority the anus and urinogenital apertures open quite separately on the surface. In the Placentalia the ureters come to open into the base of the bladder and the two oviducts join to a median vagina.

FIG. 706.

Diagrammatic horizontal section through the cloacal region of a Selachian. (After E. J. Bles.) *a*, Blind ectodermal invagination (cloacal pouch) ; *b, b'*, cloacal papilla ; *c*, peritoneal cavity, which opens by the abdominal pore at *c'* ; *Cloake*, cloaca ; *Darm*, rectum ; ***, points along the transversely striped section of the cloacal papilla at which the abdominal pore may break through, in which case the distal part of the papilla is solid (Raja).

ABDOMINAL PORES

The problem of the homology of the genital ducts in Cyclostomes and Teleostomes has been complicated by the confusion by the older authors of 'genital pores' and 'abdominal pores'. The latter name belongs to certain paired openings in the ventral body-wall in both sexes which lead from the coelom to the exterior (Bridge, **996** ; Weber, **1069** ; Ayers, **984** ; Bles, **990**). They occur somewhat irregularly in Elasmobranchs, being as a rule present only when the fish is full-grown or sexually mature, Figs. 684, 706 (Notidani, Scyllioidei, Spinacidae, Rhinobatidae, Rajidae, Torpedinidae, etc., and Holocephali). They rarely open outside (Carch-

arias), but more usually inside the cloaca on projecting papillae. Similar paired abdominal pores opening to the exterior on either side of the anus are found in Chondrostei, Polypterini, *Amia*, and *Lepidosteus*, Fig. 682 E, F. The Dipnoi also possess such pores, but they may open by a single aperture (Owen, 1839 ; Günther, 1871). Among Teleostei the Salmonidae and Mormyridae possess them. They are unknown in Amphibia, but occur in Chelonia and Crocodilia among Amniota (Moens, 1042). In no Gnathostome do the abdominal pores ever serve for the exit of genital products. It has been clearly shown by Weber that in Teleosts they may coexist with ' genital pores ' (reduced genital ducts, see p. 704).[1] Unlike genital ducts and pores the abdominal pores are not related to the dorsal region of the coelom, but are openings pierced through the body-wall at the posterior extremity of the paired ventral prolongations of the coelom passing on either side of the ventral mesentery and often called peritoneal canals. They appear to be special openings of no great morphological significance and of doubtful function. Apparently they allow fluid to escape from the coelom and perhaps to enter it ; Bles has pointed out that they usually occur in those forms which have no open peritoneal funnels on the kidney.

THE PHYLOGENY OF THE SEGMENTAL TUBULES

The phylogenetic origin of the segmental tubules from which the various genital and excretory ducts of the Craniata have been derived must now be discussed. From what has been said above about the structure and development of these organs it may safely be concluded that they are all directly or indirectly developed from segmental outgrowths of the wall of the coelom; that a pair of these funnel-like outgrowths was originally present in every segment of the body at least potentially ; that they failed to develop or have been secondarily lost in the head and tail regions ; that possibly they originally all opened separately to the exterior.

Without entering into a detailed discussion of the various theories of the origin of the coelom itself, it may be said that the only hypothesis which gives an explanation of the phylogenetic evolution of the coelom consistent with the facts revealed by a broad survey of the Triploblastic Metazoa (Coelomata) in general is the so-called ' Gonocoel Theory '. Founded on the conclusions of Hatschek and Meyer with regard to

[1] Lickteig has recently revived the view that the genital pores of Cyclostomes are abdominal pores (1035) ; but from what has been said above it appears that there is no good evidence for this interpretation.

Platyhelmia and Annelida, this theory has since been applied to all the higher Coelomata (Goodrich, 1016). It may briefly be stated as follows : In the ancestral form the genital cells tended to accumulate between the primary germ-layers, ectoderm and endoderm, and at maturity sought an escape to the exterior ; such accumulations, acquiring a definite wall from their more superficial cells, formed a pair of bilaterally symmetrical sacs ; and from the wall of each sac developed a ciliated funnel-like outgrowth which, fusing with the ectoderm (or the junction of ectoderm with endoderm), acquired an opening to the exterior. At first these sacs and funnels functioned merely as gonadial sacs and genital ducts (Platyhelminth stage) ; but soon the sacs tended to become regularly repeated along the elongated body in a bilateral series, to enlarge prematurely, and become solidly packed with genital cells only at the reproductive season (Nemertine stage). The restriction of the proliferation of genital cells to a definite region of the wall (henceforward known as the gonad proper) leads to the condition found in Annelida. Here the genital sacs become enlarged and arranged as a paired series of segmental coelomic chambers. Primitively each sac contains a testis or ovary (a proliferation from its wall), and from its wall develops a ciliated funnel (coelomostome) opening to the exterior. The coelomostomes, and the elongated coelomoducts which may develop from them, function as genital ducts.

In the majority of the segments the cavity becomes packed with reproductive cells at maturity; but, owing to increasing specialisation and differentiation between segments, some of the more anterior and posterior usually become sterile, failing to develop gonads. Thus, not only do the sacs tend to develop prematurely as chambers filled with fluid, but some of them remain in this condition. This is due to the acquisition of new functions. The coelom becoming a spacious cavity serves to distend the body-wall and afford a place in which the viscera can expand, spread, and indulge in muscular movements. Moreover, it also acquires an excretory function. In the metamerically segmented Annelida and Arthropoda this leads to a division of labour between the segments. In some the coelomoducts are devoted to excretion, in others they retain their primitive rôle of genital ducts. Moreover, in Arthropoda each sac, in the majority of segments, becomes subdivided into a dorsal genital and a ventral excretory portion. The genital portions usually combine to form the adult ' ovary ' or ' testis '. A varying number of the segmental ventral portions persist as the excretory organs in most Arthropods. In the unsegmented Mollusca the history of the paired coelomic cavities, coelomostomes and coelomoducts, is essentially similar ; but here the differentiation arises between different parts of the same coelomic sac,

which tends to become subdivided into genital, perivisceral (pericardial), and excretory compartments. The same general development of the coelom and coelomostome can be traced in all the groups of Triploblastic Invertebrata.

Turning now to the Vertebrata we find similar paired coelomic sacs developed from the mesoblast. Primitively they arise as separate segmentally disposed sacs from whose walls develop the gonads. Primitively also they were in all probability all of them fertile (as they still are to a great extent in *Amphioxus*); but anteriorly and posteriorly they become sterile. When, as in Craniates, the cavities of the segmental sacs became confluent ventrally even in the embryo (lateral plate region) the gonads combined to longitudinal paired bands showing little or no trace of segmentation. But, excepting in the head and tail regions, every segment still produced a pair of funnel-like outgrowths or coelomostomes, and these may still convey the genital products to the exterior. In the male Gnathostome this primitive function is performed by coelomostomes belonging to quite a large number of segments; in the female the ducts are apparently of the same ultimate origin, but their metameric composition is obscure, and they represent perhaps the coelomoducts of only one segment.

Unfortunately theories of the morphology of the segmental tubules of the Vertebrates and of their origin from comparable organs in the Invertebrates were put forward and generally accepted before the structure and development of these organs had been correctly described or was understood. It was Semper who first definitely maintained that the Vertebrate tubules are homologous with the nephridia of Annelida. This attractive view was almost universally accepted at a time when almost any tube leading to the exterior was called by the convenient name 'nephridium'. But Semper's theory seems to be based on deceptive resemblances and erroneous interpretations. It is now well established that the Vertebrate tubules are coelomic in origin, of centrifugal growth, and that the ectoderm takes no share in their formation. On the other hand, it is now held that the nephridia are never of coelomic origin, are of centripetal growth from the surface, and probably always derived from the ectoderm, or at least from superficial cells. At first the nephridia have blind inner ends provided with flame-cells or solenocytes (protonephridial stage), and have nothing to do with the gonadial sacs (Platyhelminth and Nemertine stages).

But when the latter become large coelomic sacs the nephridia perforce are pushed into them, become related to them in excretion, and remain in the adult as the main excretory organs (Annelid stage). In some rare cases they may open into the coelom by nephridiostomes and lose the

solenocytes (Oligochaeta, some Polychaeta).[1] But in the great majority of the Invertebrate Coelomata the nephridia appear only in early stages of development and are lost in the adult (Mollusca, Phoronidea, etc.), or do not appear at all (Arthropoda, Echinoderma). Thus, in the Invertebrates the nephridium is but rarely preserved as an adult excretory organ ; while the coelomostome is constantly present in all groups as a genital and often as an excretory duct as well.——

It is clear that, if the vertebrate tubules are to be compared with any of the organs of an Invertebrate, it is not with the nephridia but with the coelomostomes that they must be homologised.

The argument would be clinched could we point to a Vertebrate possessing both well-developed nephridia and coelomic tubules. Unfortunately no such form is known to exist at the present day. The Craniates have preserved the coelomostomes, but lost the nephridia,[2] no longer necessary since the former have taken on the function of excreting. On the other hand, the Cephalochorda have preserved the nephridia (Boveri, Weiss), which are now known to be of typical protonephridial structure without internal openings and provided with well-developed solenocytes (Goodrich, 1017). But the genital ducts of the Cephalochorda appear to have been lost, the genital cells escaping by bursting through the wall of the genital sacs into the atrium.[3]

One more point remains to be considered : If the segmental tubules of the Vertebrates are homologous with the genital ducts of other Coelomata, is it the peritoneal funnel or the nephrocoelostome which represents the primitive coelomostome ? Many embryologists consider that the cavity

[1] In the vast majority of the Coelomate Invertebrates the nephridia and the coelomostomes have nothing to do with each other. In one class only, the Polychaeta, a connexion may be established between them, leading to the formation of a complex organ (nephromixium) serving for the exit of both excretory waste and genital products (Goodrich, 1899–1900). But even in this class there are forms where these organs retain their primitive independence (Capitellidae, Nereidae).

[2] Unless, indeed, these are represented by the thymus, as held by van Wijhe.

[3] A vestige of the primitive coelomostome may, however, be represented by the small knob or 'hilum' formed by the fusion of the mesodermal wall of the genital sac with the atrial epithelium at the point where the rupture takes place. A somewhat similar reduction of the genital ducts to mere pores has been described above (pp. 704-7) in Teleostei and Cyclostomes. Among Invertebrates also the coelomoducts may be much reduced to quite short funnels or pores (oviducts of many Oligochaetes, genital funnels of many Polychaetes). Or, just as in *Amphioxus*, these vestigial ducts may cease to open to the exterior, the genital products bursting through the body-wall; some Polychaeta (such as epitokous forms among Nereidae, etc., and *Clistomastus* among Capitellidae).

of the intermediate cell-mass or stalk of the somite (which becomes the cavity of Bowman's capsule, and is often called the nephrocoele) is a chamber of the coelom itself. In this case the nephrocoelostome would be the coelomostome opening from it, and the peritoneal funnel a specialised narrow channel of communication between this still segmental chamber and the general ventral splanchnocoele. On the other hand, the peritoneal funnel may be the coelomostome and the chamber a specialised enlargement of the coelomoduct into which penetrates the glomerular blood-vessel. Or, again, if the nephrocoelostome is the original funnel, it might by extension ventrally give rise to the peritoneal funnel as well. There is something to be said for each of these interpretations, and at present it seems scarcely possible to decide between them.

CHAPTER XIV

PERIPHERAL NERVOUS SYSTEM AND SENSE ORGANS

THE PERIPHERAL NERVOUS SYSTEM

THE nervous system has been evolved to conduct nerve-impulses. Sensory impulses are due to the action of stimuli from the external and internal environment on receptor sensory cells on the surface of the body or in its deeper tissues and organs; they are conveyed to the central nervous system, where they set up excitor or motor impulses which are transmitted to effector cells and organs, the muscles, and glands. Thus appropriate responses are called forth, and the various functions of the organism are integrated to its advantage. The complex system of interconnecting peripheral nerves convey the sensory impulses to and excito-motor impulses away from the central nervous system where these impulses are co-ordinated. The central nervous system consists of the brain and spinal cord situated dorsally, while the peripheral nervous system is made up of

ganglia and nerves distributed to all parts of the body. The essential elements of which nervous tissue is composed are the neurons or ganglion cells, with their branching conducting processes or fibres, of which the longest is called the axis-cylinder, axon, or neurite, and the others the dendrites. Both axon and dendrite may end in fine twigs for receiving or transmitting impulses. The neuron receives impulses by its dendrites and transmits them by its axon. Usually the axon does not divide till at or near its destination. The nerve-impulse passes from neuron to neuron, where the tips of the processes of one neuron meet the cell-body or processes of another. At this point of junction, known as the synapse, there would appear to be mere contact and not actual permanent continuity of the conducting fibril.[1] According to the ' Neuron theory ' of His and Waldeyer, now generally accepted, the whole nervous system, with the possible exceptions mentioned below, consists of chains of such neurons along which the impulses can pass when they overcome the resistance offered by the synapse. While it seems certain that the bulk of the nervous system, at all events of the Craniata, is built on this plan, yet there remain certain delicate nerve-plexuses on the blood-vessels, under the mucous membrane of the buccal cavity (of Amphibia and probably other forms), and in the wall of the gut, which apparently do not conform to it (Bethe, 1903 ; Prentiss, 1904 ; E. Müller, 1151-2). In these cases it seems possible that a true nerve net exists of anastomosing fibrils continuous from cell to cell, such as commonly occurs in the lower Invertebrata. In addition to the true nervous elements there are in the central nervous system packing neuroglia cells, and sheath cells on the fibres of the peripheral nerves. The nerves of anatomy are made up of bundles of such axons and their sheaths, the cell-bodies of the neurons being usually gathered either in the central nervous system or in ganglia outside it.

The first generalisation of importance, then, is that the peripheral nerves consist of two sets of nerve-fibres : one set of sensory or afferent fibres whose function is to carry impulses centripetally to the central nervous system, and another set of excito-motor or efferent fibres whose function is to carry impulses centrifugally from the central nervous system to muscles and glands. A nerve may be composed of either or of both kinds of fibre, Fig. 744.

It has already been explained (Chapter V.) that every segment of the body of a Vertebrate is primitively provided with a pair of dorsal and of ventral nerve-roots by which the nerve-fibres pass to or from the central nervous system. Moreover, every segment contains a pair of mesoblastic

[1] Whether the conducting fibril or substance is or is not ever continuous from one neuron to another is, however, still a matter of dispute.

segments, from each of which are developed a dorsal myotome and ventral lateral plate (p. 4). From the myotomes, which retain more or less their original segmentation, are derived the segmental muscles or myomeres of the adult (also the hypoglossal musculature, and the muscles of median fins and paired limbs). From the lateral plates, which lose their segmentation by longitudinal fusion either very early (*Amphioxus*) or from the very first (most Craniates), is derived the 'unsegmented' lateral plate mesoblast; this (together with mesoblast derived from sclerotome outgrowths of the dorsal region) gives rise to all the mesoblastic tissues of the body, excepting the myomeres. From these tissues, generally denoted as the unsegmented mesoblast, are therefore developed the contractile elements of the vascular system, certain muscles of the skin, the whole of the musculature of the alimentary canal and its appendages including the visceral muscles of the jaws and gill arches, and of the urinary and genital organs.

Returning to the description of the peripheral nerves, we find that primitively, as in *Amphioxus* and the Petromyzontidae, the dorsal and ventral roots are independent nerves; that in all Gnathostomes and in the Myxinoidea the dorsal and ventral nerves of a segment combine on each side in the spinal region to form compound spinal nerves each with a dorsal and a ventral root;[1] that in the cranial region the dorsal and ventral nerves remain separate.[2] Further important generalisations may be made: that the afferent fibres all reach the central nervous system by the dorsal roots, and that the cell-bodies of these sensory neurons are all situated in the segmental, cranial, and spinal ganglia outside the neural canal on these roots (except in *Amphioxus*); that the efferent fibres may pass out by both the dorsal and the ventral roots, and that the cell-bodies of these excito-motor neurons are all situated inside the central nervous system, with the exception of those belonging to the 'sympathetic' system as explained below (p. 772). It follows that while the ventral roots are, so far as we know, purely efferent, the dorsal roots may be of mixed character, Figs. 707, 747.

Although it must be supposed that originally the dorsal roots all along the body contained both afferent and efferent fibres, as they do in *Amphioxus*, a divergence has come about in the Craniata between the segmental

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[1] These primary segmental roots must not be confused with the secondary rootlets into which they may be differentiated; for in the higher Craniata the fibres of the various components of the cranial nerves may become gathered together and more or less separated into distinct rootlets. Thus the rootlet of the visceral motor component is often confused with a primary ventral motor root.

[2] Except in so far as they may be connected by sympathetic fibres.

roots of the head and of the rest of the body ; so that while the dorsal cranial nerves of Craniates contain efferent fibres, they are stated to be totally absent from the dorsal roots of their spinal nerves, Figs. 745, 750. From time to time, however, it has been maintained that efferent
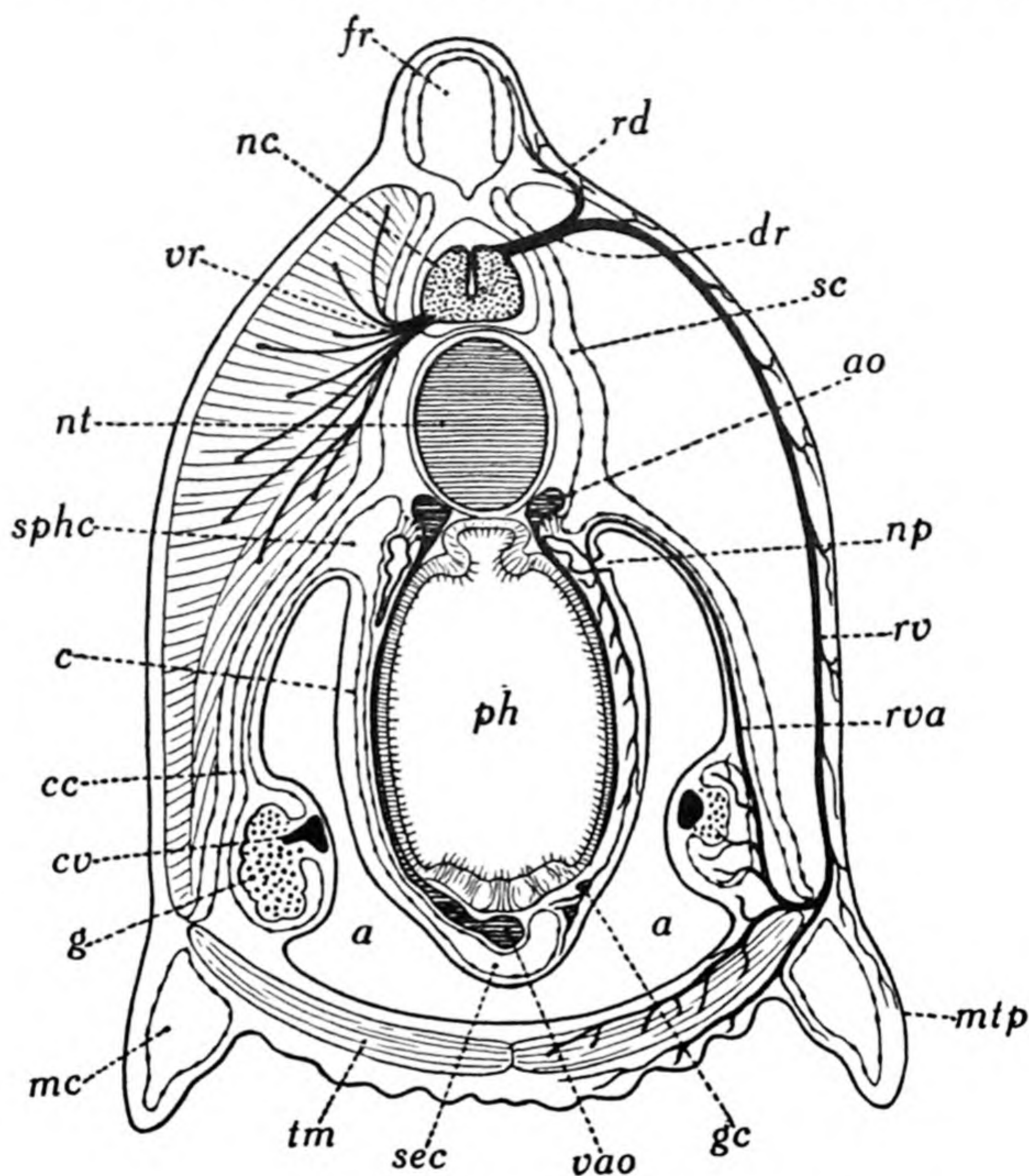
FIG. 707.

Diagrammatic transverse section of *Amphioxus* in pharyngeal region, showing peripheral nerves, coelomic cavities, etc.   Primary gill-bar on left, secondary on right.   *a*, Atrium ;   *ao*, lateral dorsal aorta ;   *c*, coelomic canal in primary bar ;   *cc*, coelomic canal ;   *cv*, posterior cardinal vein ;   *dr*, dorsal root nerve ;   *fr*, fin-ray ;   *g*, gonad ;   *gc*, ganglion cell ;   *mc*, metapleural cavity ;   *mtp*, metapleure ;   *nc*, nerve-cord ;   *np*, nephridiopore ;   *nt*, notochord ;   *ph*, pharynx ;   *rd*, ramus dorsalis ;   *rv*, ramus ventralis ;   *rva*, ramus ventralis ascendens ;   *sc*, sclerocoele ;   *sec*, subendostylar coelom ;   *sphc*, lateral suprapharyngeal coelomic chamber ;   *tm*, transverse subatrial muscle ;   *vao*, ventral aorta ;   *vr*, ventral root nerve.

fibres (vasomotor ?) issue through the spinal dorsal roots ; future research may perhaps show that the primitive efferent component remains, at all events, in some of the lower forms (*Amphioxus*: Willey, 94 ; Heymans and v. d. Stricht, 1122 ; Dogiel, 1104 ; Kutchin, 1141 ; Franz, 1109).

Amphioxus has no well-defined ganglia on its dorsal nerves, for the nucleated cell-bodies of the afferent fibres are still inside the spinal cord or

scattered along the root of the nerve to near its bifurcation (Rohde, **1169**; Hatschek, 1882 ; Johnston, **1127**).[1]

Concerning the general function and distribution of the sensory fibres it may here be mentioned that Sherrington distinguishes three main reception fields : the superficial extero-ceptive field receiving stimuli from the external world, the intero-ceptive field receiving stimuli at the inner surface of the alimentary canal, and the deep proprio-ceptive field
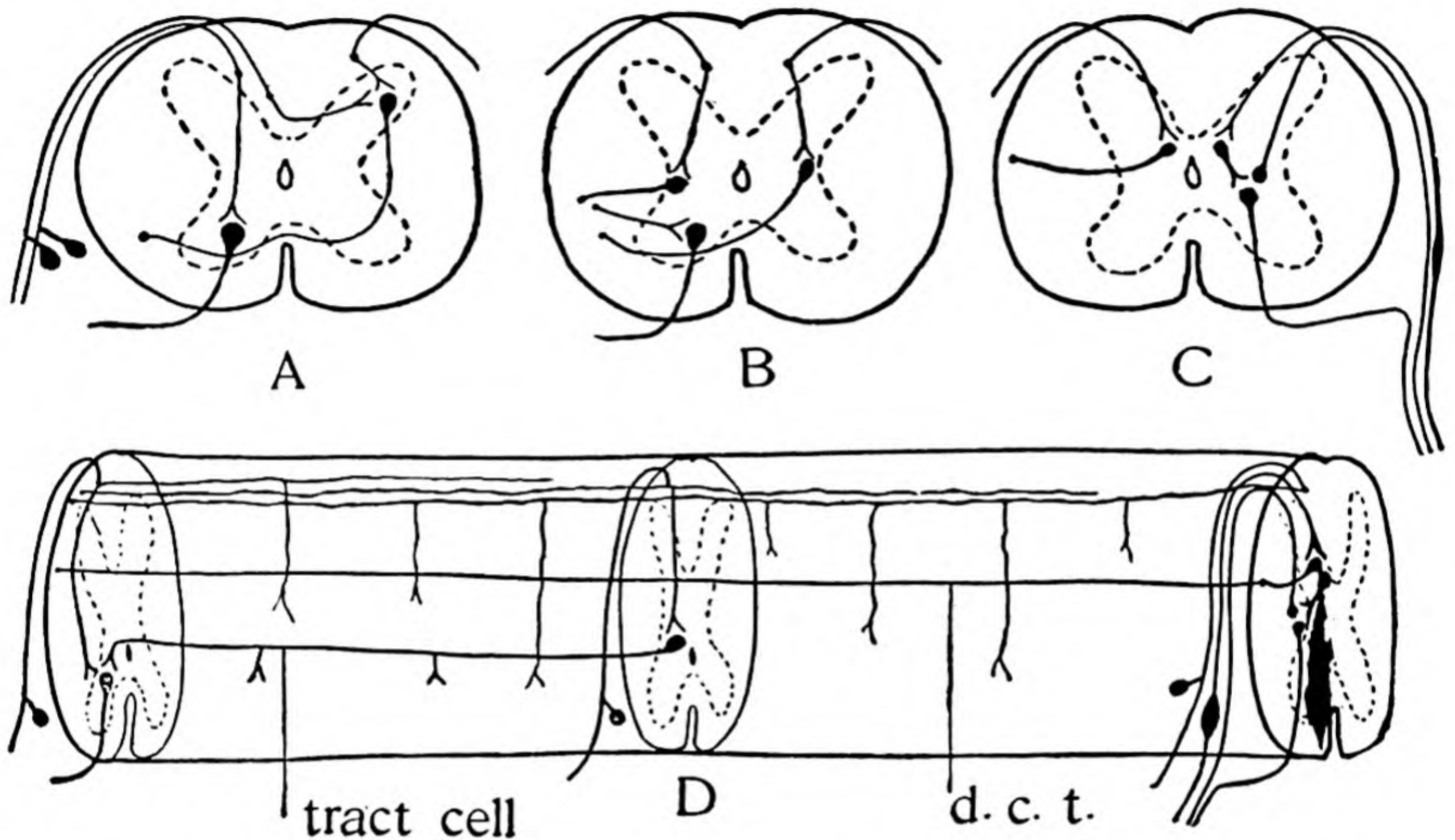
FIG. 708.

Diagrams illustrating several forms of reflex chains (from J. B. Johnston, *Nerv. Syst. of Vert.*, 1908). A, Somatic sensory and motor ; B, by way of tract cells ; C, visceral sensory and motor ; D, spinal cord and nerve roots from side. *d.c.t*, Direct cerebellar tract.

receiving stimuli from the tissues and organs in the body. In each of these fields stimuli may directly affect the terminal branches of sensory fibres, free nerve-endings ; or be received by special sensory cells or characteristic sense organs containing sensory cells specialised to respond to particular stimuli.

The afferent and efferent fibres, then, serve as paths for ' reflexes ' or reflex arcs completed through the brain or spinal cord. The nerve-impulse passes along a chain of neurons ; entering by the sensory neuron, whose body is in the segmental ganglion, and emerging by the excito-

[1] It should also be noticed that in *Amphioxus* the sensory cells in the epidermis are said to send conducting fibres directly to the central nervous system, as in the Invertebrata ; whereas in the Craniata the sensory impulses, except in the case of the nasal olfactory epithelium, are transmitted by the axons of afferent neurons whose distal branching extremities are closely related to the sensory cells. In these respects *Amphioxus* seems to be, as in so many of its characters, more primitive than the Craniata.

motor neuron, whose body is in the central nervous system, Figs. 708, 747. The connexion between these two is made by one or more intermediate neurons situated entirely in the central nervous system (except in the case of the 'sympathetic' system, see below, p. 772). The behaviour of vertebrates is to a great extent made up of the co-ordination of such reflexes.

Lastly, an important point remains with regard to the function of the dorsal and ventral motor fibres (leaving out of account those belonging to the 'sympathetic' system); those of ventral roots supply only the muscles derived from the dorsal segmented myotomes (including, of course, the eye-muscles, hypoglossal muscles, and limb-muscles); while the motor fibres issuing by the dorsal roots innervate only the musculature derived from the ventral unsegmented mesoblast derived from the lateral plate.

The segmental value of the cranial and spinal nerves has been already dealt with above (Ch. V.). While comparative anatomists and embryologists were working out this interesting problem, other observers were studying the peripheral nerves more from the point of view of the function of the various neurons, and the peripheral distribution and central connexions of the fibres. Great advances have been made since the introduction of the silver impregnation technique of Golgi, the methylene blue staining of Ehrlich, and Waller's method of tracing the path of degenerating fibres severed from their cell-bodies. By these new methods, together with that of the artificial stimulation of nerve-fibres in the hands of many skilful experimentalists, the course of most of the important sets of fibres has been made out. Gaskell in 1886 also traced their origin and distribution by their histological characters, distinguishing somatic from splanchnic or visceral fibres (Merritt, 1147).

A new impetus was given to the comparative study of the functional components of the nervous system by the work, more especially, of Strong, who in 1895 made a complete analysis of the cranial nerves of the larval amphibian by the reconstruction of serial sections. Since then Strong (1176), Herrick (1120-21), Johnston (1126-30), Norris (1155-8), Willard (1184), and others have successfully applied the method to various Vertebrates from *Amphioxus* upwards. These detailed researches combined with the more purely anatomical studies of the older anatomists, such as Stannius (1849) and Fischer, 1843–54, and the modern work of Ewart and Mitchell on Selachians (1107), of Allis on *Amia* and other fishes (402, 404-5, 1081-5), and of Fürbringer (340), have helped to build up the important doctrine of Functional Components, of which the chief conclusions may now be summarised as follows :

The peripheral nervous system contains four chief components, two

sensory and two excito-motor, each subserving special functions, related to special ' end-organs ', and connected to four corresponding longitudinal regions of the central nervous system. These regions appear in the spinal cord in the form of ' columns ', of which the two sensory are dorsal and the two motor ventral, and extend forward into the brain, where, however, they become much modified and complicated in higher forms. The four component systems are known as the Somatic Sensory, the
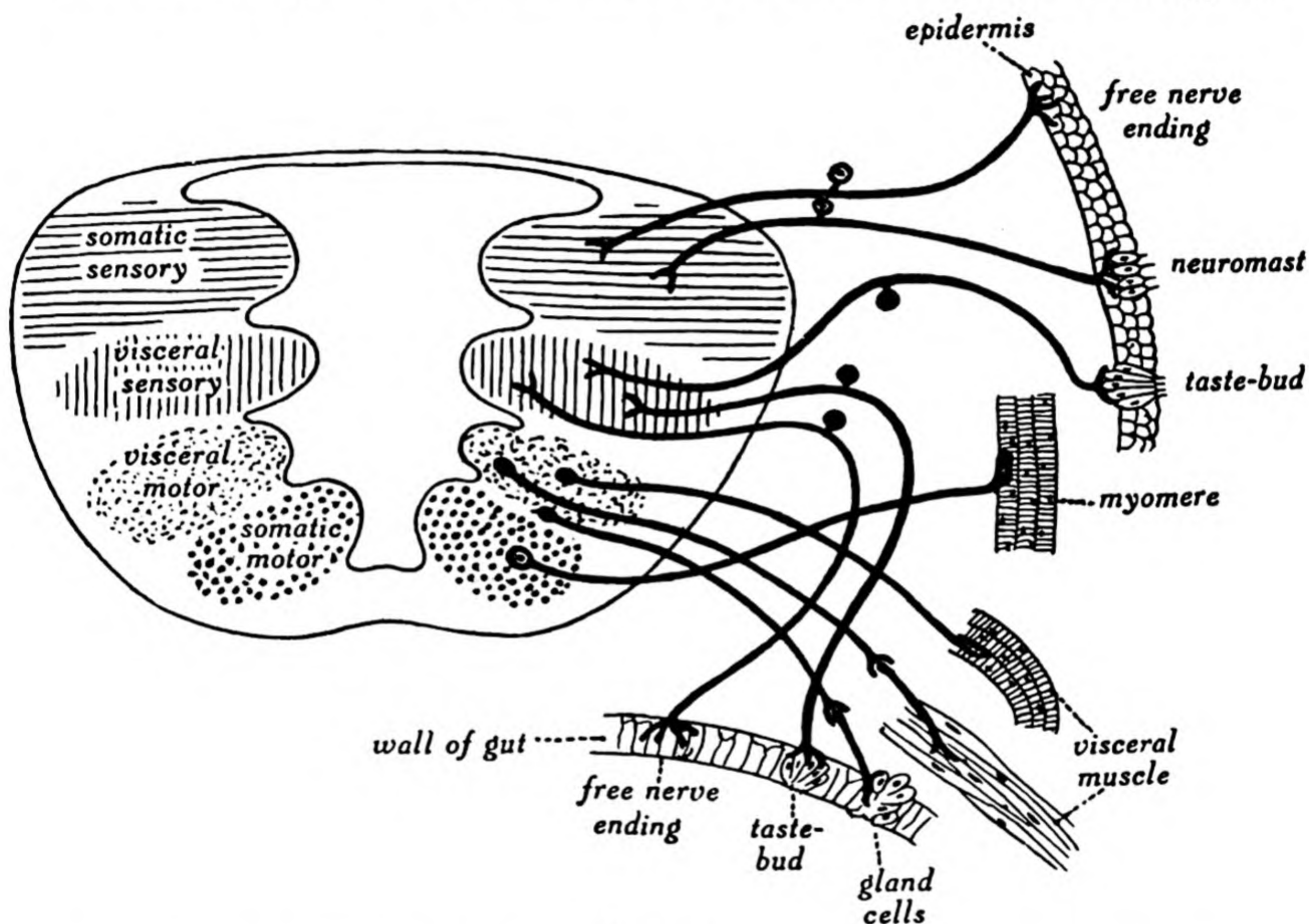
FIG. 709.

Diagram showing central origin from medulla and peripheral distribution of systems of *nerve-components*.

Visceral Sensory, the Visceral Excito-motor, and the Somatic Motor, Fig. 709.

Speaking generally, the somatic components are chiefly concerned with responses to the animal's external environment, while the visceral components are chiefly concerned with responses to its internal environment ; that is to say, with the internal processes of digestion, respiration, circulation, excretion, and reproduction. But no hard-and-fast line can be drawn between them on this account.

The primary sensory components may become subdivided owing to each developing characteristic sense organs, such as the lateral-line organs related to the Somatic Sensory component, and the taste-

buds related to the Visceral Sensory. The fibres belonging to each system present in a nerve are known as the components of that nerve, Fig. 728.

The functional divisions of the nervous system and components of the Craniata may be further described as follows :

A. **Somatic Sensory System.**—1. *General cutaneous* : Afferent fibres from the whole epiblastic surface of the body, the extero-ceptive field ;
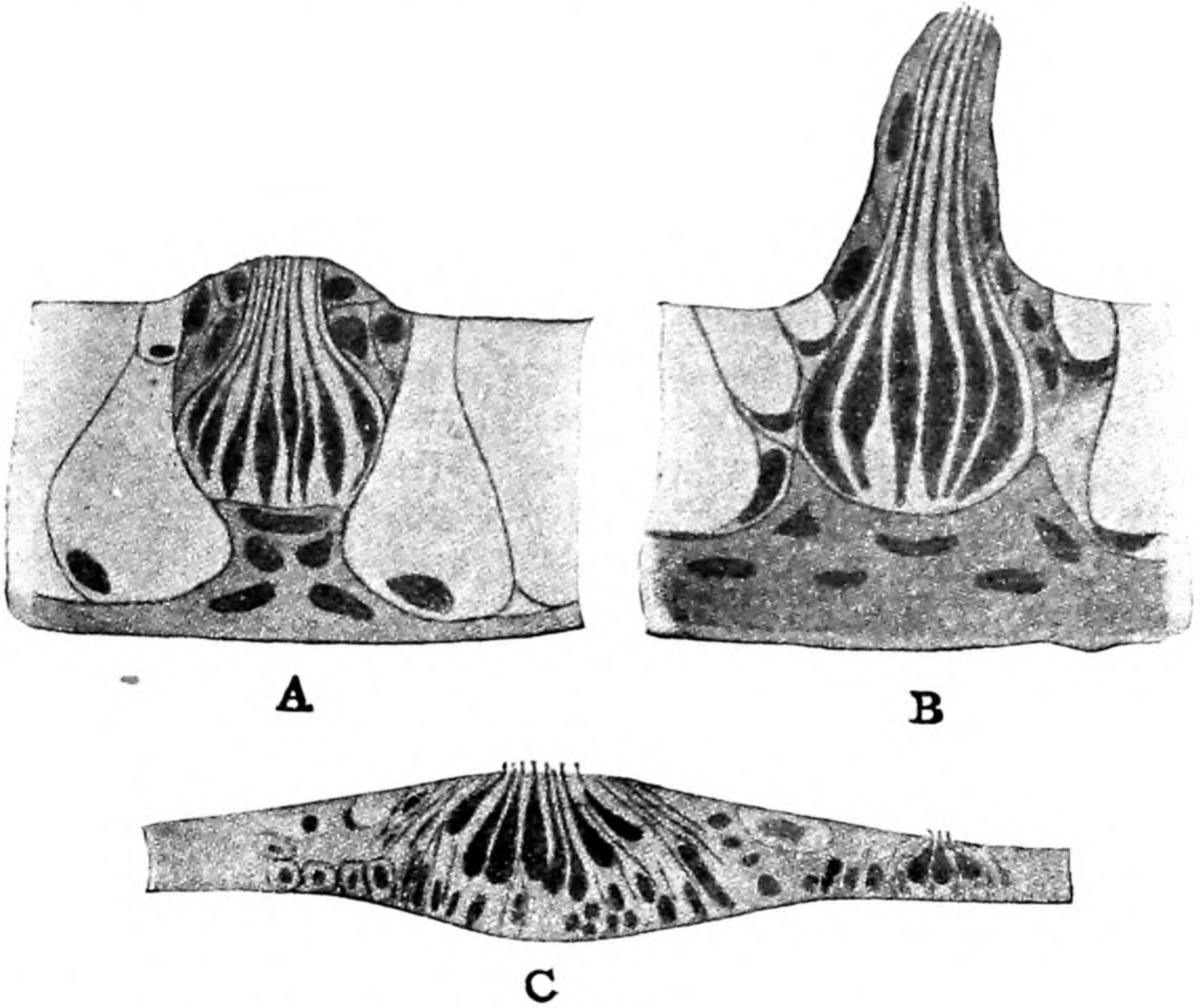
FIG. 710.

A, Taste-bud from oesophagus of *Catostomus* at time of hatching; B, taste-bud from pharynx of same; C, two neuromasts from skin of same. (From J. B. Johnston, *Nerv. Syst. of Vert.*, 1908.)

with ' free nerve-endings ' among the epidermal cells, and more specialised end-organs, such as the corpuscles of Meissner and of Merkel, the end-bulbs of Krause, etc. These receptors are stimulated by pressure and vibrations (touch, radiant heat, light, cold, and pain). The cell-bodies of the neurons are in the cranial and spinal ganglia, and the fibres distributed primitively in every segment of the body by the dorsal cranial, and the spinal nerves (nervi profundus, trigeminus, facialis, glossopharyngeus, vagus, et spinales). The central connexions are with the dorsal horn or column of the spinal cord and its continuation in the brain, with associated

' nuclei ' (tractus spinalis trigemini of medulla oblongata, nucleus funiculi, n. acusticum, cerebellum, etc.).

2. The special visual organs, paired lateral eyes and dorsal pineal organs, were probably evolved from this system; but were differentiated and have remained within the original wall of the brain.

3. *Special cutaneous or acustico-lateral system*: Afferent fibres related to neuromasts or organs of the ' lateral line ' (also pit-organs and ampullae), receptors in aquatic forms of relatively slow vibrations. Neuromasts possess superficial pear-shaped sensory cells which do not extend through the whole depth of the epithelium and bear sensory hairs on their outer surface, Figs. 710, 713.

The auditory organ represents a specialised region of the Special Cutaneous system, often therefore called the acustico-lateral or more shortly the lateralis system.

The acustico-lateral fibres are distributed typically by the facial, auditory, glossopharyngeal, and vagus nerves; and their central connexions are chiefly with the nucleus acusticum and n. funiculis, and cerebellum.

This acustico-lateral system is dealt with more in detail below (p. 732).

4. With the General Cutaneous system may be associated the related afferent fibres of the ' muscular sense ' of the proprio-ceptive field. They have fine nerve-endings among the mesoblastic tissues, bones, tendons, and muscles, also Golgi organs and Pacinian bodies. The ' muscle spindles ' of striated muscle fibres derived from myotomes and from the lateral plate are end-organs of this system. The course of these fibres and their central connexions are similar to those of the General Cutaneous system.

B. **Visceral Sensory System.**—1. *General visceral*: Afferent fibres from the lining of the alimentary canal, the intero-ceptive field; with free nerve-endings responding to mechanical stimuli. The cell-bodies of the neurons are in the dorsal cranial ganglia of the facial, glossopharyngeal, and vagus nerves, and the fibres are typically distributed in their visceral branches. The afferent fibres enter the central nervous system by the morphological dorsal roots and connect with the fasciculus communis or solitarius, lobus vagi, l. fascialis, and associated centres, and Clarke's column in the spinal cord. Sometimes known as the splanchnic or the communis system.

2. The special paired olfactory organ, whose sensory cells send conducting fibres to the bulbus and tractus olfactorius, should probably be considered as belonging to this system. Affected by chemical stimuli, the olfactory organ may have been primitively intero-ceptive; but in most Craniates it acts chiefly as an extero-ceptor.

3. *Special visceral*: Afferent fibres related to taste-buds (end-buds),

typically situated on the mucous surface of the buccal cavity and pharynx, Fig. 710. Groups of special sensory cells whose bodies extend through the whole depth of the epithelium form these taste-buds which are receptors of chemical stimuli (from sweet, sour, salt, and bitter substances). The fibres enter the brain by visceral branches of dorsal cranial nerves (facial, glossopharyngeal, and vagus), the cell-bodies of the neurons are in their ganglia, and the central connexions are with the same centres as those of the General Visceral system (p. 730).

4. Associated with the General Visceral sensory system are afferent fibres travelling in the 'sympathetic' nerves (p. 770). They have free nerve-endings among the smooth muscle-cells and glands supplied by the 'sympathetic' system.

C. **Somatic Motor System.**—Efferent fibres issuing by ventral roots and supplying all the musculature derived from the segmental myotomes. These are the myomeres or body-wall muscles of the tail and trunk, and their derivatives the muscles of median and paired fins and limbs ; the muscles of the Mammalian diaphragm ; the dorsal epibranchial muscles of Elasmobranchs ; the hypoglossal musculature connected with the branchial arches and tongue and derived from certain myotomes of the gill region (ventral hypobranchial muscles, etc.) ; the external muscles of the eye-ball (modified anterior myotomes). The end-organs are the 'motor end plates' on the muscle fibres which are all striated. The cells giving origin to these somatic motor fibres are in the ventral horn of the spinal cord, and the corresponding nuclei of the hypoglossal, abducens, oculomotor, and trochlear cranial nerves. Their action is under the control of the will.

D. **Visceral Motor System.**—1. *Special visceral motor* : Efferent fibres, issuing by dorsal roots, and supplying muscles derived from the lateral plate mesoblast. These are the visceral constrictor muscles and their derivatives, including the muscles of the jaws, various muscles of the hyoid and branchial arches, and trapezius. The end-organs are 'motor end plates' on the muscle fibres which are striated. They are under the control of the will, and the cell-bodies are situated in the lateral horn or intermediate zone of the medulla. The fibres issue by the trigeminal, facial, glossopharyngeal, and vagus (including the spinal accessory) cranial nerves.

2. 'Sympathetic' or Autonomic excito-motor system of efferent fibres supplying glands and muscles (mostly unstriated and derived from the lateral plate mesoblast), and issuing by both dorsal and ventral roots. This system is described below.

This analysis of the peripheral nerve-fibres into components according

to the function and distribution of their receptor and effector end-organs, and to their connexion with longitudinal zones of the central nervous system, has thrown much light on the structure and evolution of the nervous system in Vertebrates. Passing from *Amphioxus* to Man we can trace the rise or the loss of components. It offers an intelligible explanation of the great variation in the number and size of their nerve-branches within even small groups. For a nerve varies according to the number of fibres of the components contained in it, and these again according to the abundance of the end-organs they supply. Not only the size but the very presence or absence of a nerve in a particular animal depends on whether these end-organs are developed and needed for its life. Nevertheless, there are weak points in the classification of the components in four main systems, and some of them fit with difficulty into the classification adopted by physiologists. Especially is this so with some of the visceral components, which are better treated separately (see 'Sympathetic' System, p. 770).

Taste-bud System.—There are points of interest concerning the Special Visceral or Taste-bud system. In the terrestrial Vertebrates the taste-buds are restricted to the internal lining of the anterior region of the alimentary canal. For instance, in Mammalia they are scattered over the tongue, especially near the circumvallate and foliate papillae, on the soft palate, and sparsely on the larynx and epiglottis. Of these the more abundant anterior buds are supplied by the facial nerve, the most posterior by the vagus, and some intermediate ones by the glossopharyngeal. In most fishes they occur distributed over the roof, sides, and floor of the buccal cavity and pharynx (in some Teleosts even in the oesophagus). But in *Petromyzon* they may also be found in the adult on the outer surface of the head and branchial region (Johnston, 1128). In adult Gnathostomes they also tend to spread over the external surface (Herrick, 1120 ; Johnston, 1129). *Amia*, many Teleostei, and some Amphibia have taste-buds not only internally, but also scattered over the head ; in some Teleosts (such as Siluriformes and Gadiformes) they extend to the base of the fins, and finally over the whole body including the tail. This great increase in the area of distribution of taste-buds is, of course, accompanied by a corresponding increase in this component of the facial nerve, Fig. 711, and of its centres in the brain (Herrick, 1121). In these aquatic forms the external taste-buds become extero-ceptive organs for the search of food.

Now the question arises whether these sense organs are really of endodermal origin and have spread outwards through the mouth by an outgrowth of endodermal tissue ; or are ectodermal organs which developed

originally in that part of the buccal cavity derived from the stomodaeum and consequently lined by ectoderm. Thence, by growth of ectodermal tissue (possibly also through the gill-slits), they might have spread backwards into the pharynx and outwards over the body.[1] In this connexion it is interesting to note that excepting for taste-buds no receptor cells are known to occur in the endodermal lining of any Vertebrate ; and, since it is generally held on good evidence that all sensory and nervous cells are ultimately derived from the ectoderm (p. 757), it would require very rigid proof to establish that the taste-buds are an exception to this rule. Unfortunately, it is not possible accurately to determine the limit between ectoderm and endoderm in the buccal cavity of Craniates in the adult or
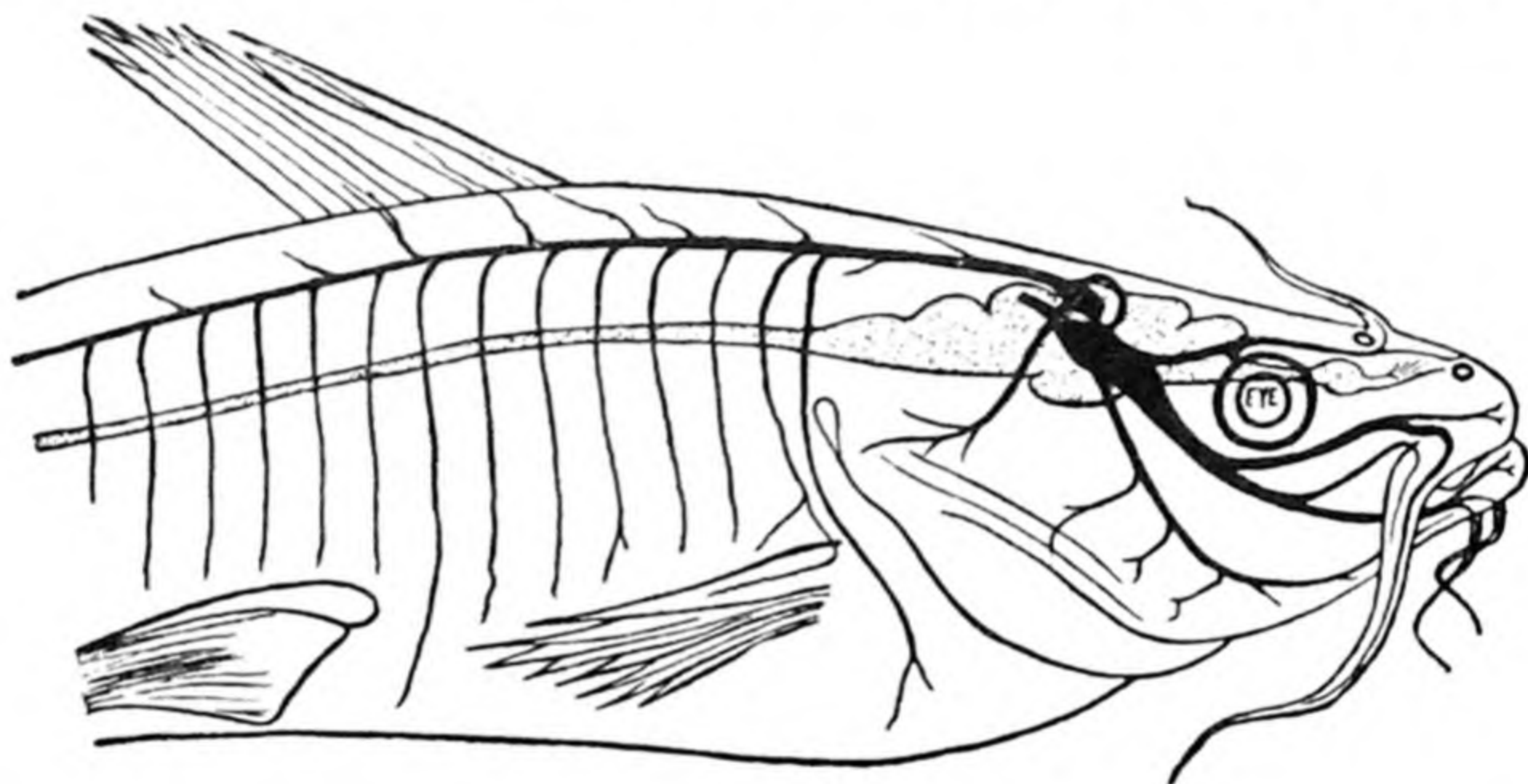
FIG. 711.

Cutaneous gustatory branches (special visceral component) of facial nerve of *Ameiurus* (after C. J. Herrick, from J. B. Johnston, *Nerv. Syst. of Vert.*, 1908).

even soon after the mouth has broken through, as all trace of the oral separating membrane usually disappears. No doubt the position of the hypophysial invagination indicates an ectodermal area, but with rare exceptions (*Polypterus*, p. 235) the connexion does not persist and the hypophysis is indeed separated off at a quite early stage of development. Dorsally, however, the limit is probably at the pituitary region. The same difficulty applies to the limit between the ectoderm and endoderm in the gill-slits. It may therefore be argued that ectodermal cells migrate into the endodermal lining of the pharynx even perhaps before the breaking through of the mouth or slits. Nevertheless, it seems highly probable that the taste-buds first arose in the endoderm and spread through the mouth on to the surface of the body. This is the view maintained by Johnston (1129), who finds that in *Petromyzon*, and the Teleosts *Catostomus* and *Coregonus*, they occur in the young only in the pharynx, and appear

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[1] Such a spreading of the area supplied by a sensory component commonly occurs (see pp. 743 and 747).

afterwards on the lips, then on the head and body. Landacre (1142) believes the internal taste-buds to be of endodermal and the external
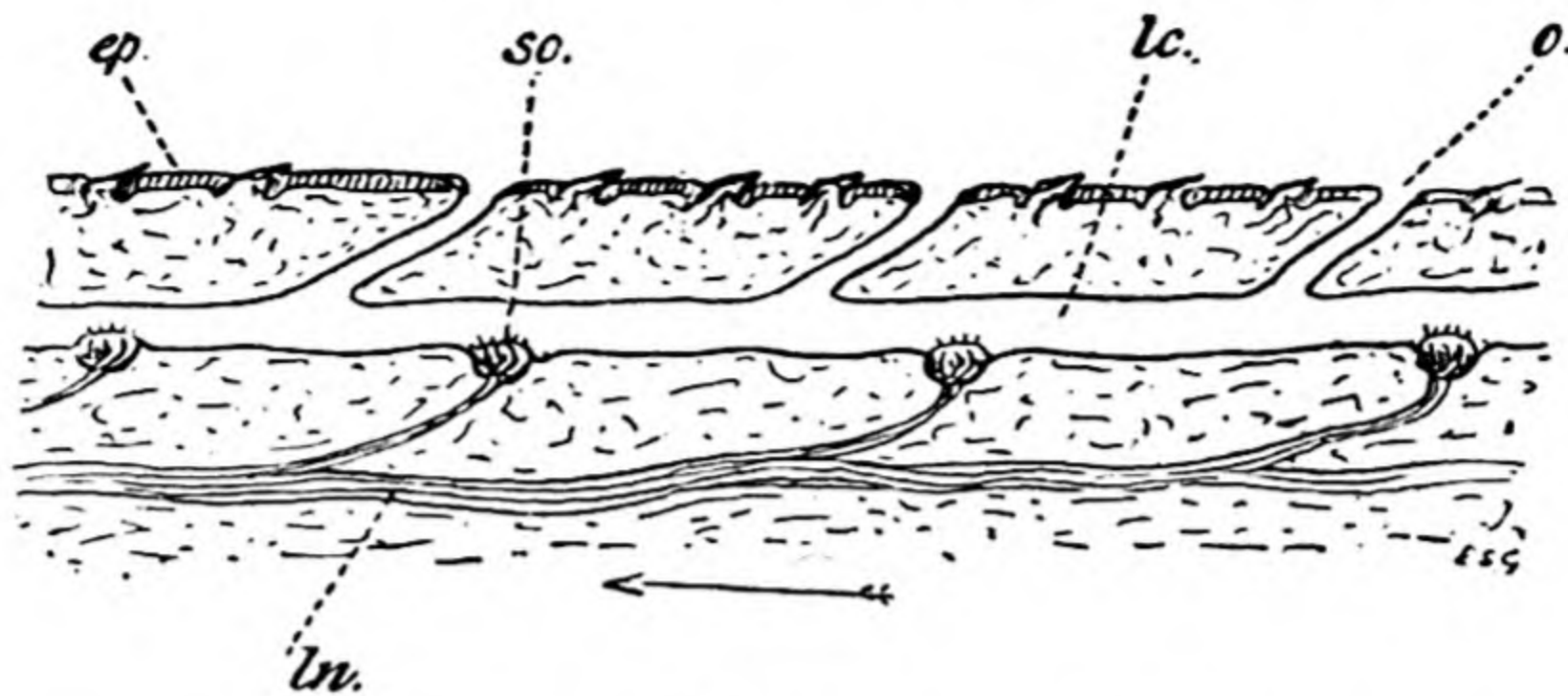
FIG. 712.

Diagram of the lateral-line canal of a Selachian seen in a section vertical to the surface. *ep*, Epidermis ; *lc*, longitudinal canal ; *ln*, lateral-line nerve ; *o*, opening of branch canal on surface ; *so*, sense organ. (From Goodrich, *Vert. Craniata*, 1909.)

(sometimes distinguished as ' terminal buds ') to be of ectodermal origin in *Ameiurus*. Cook and Neal (1102), after a careful study of the development of *Squalus*, support Johnston's conclusion. This view is easier to adopt if, as held by Botezat (1910) and G. H. Parker (1912), the taste-buds
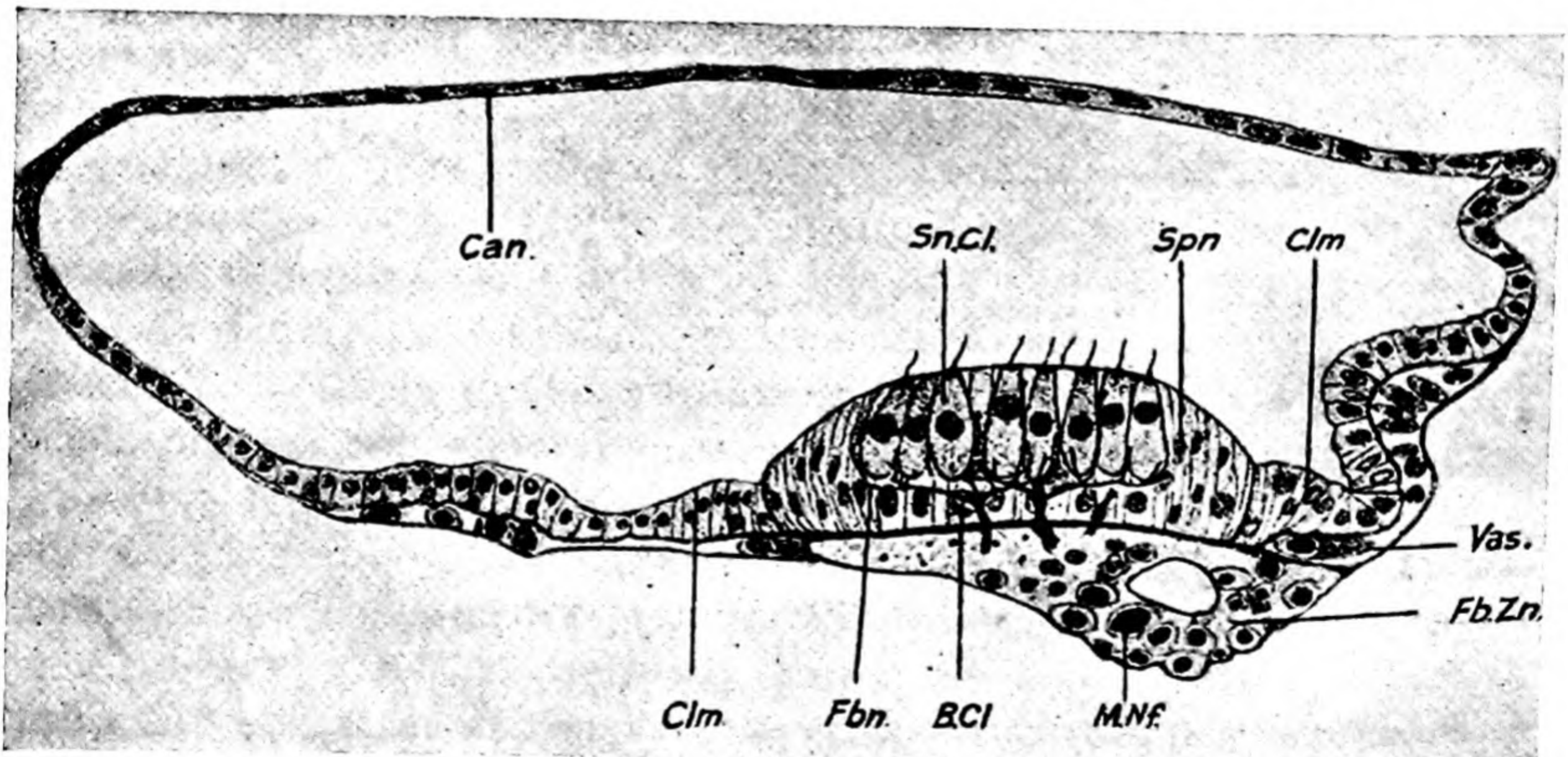
FIG. 713.

Transverse section of lateral-line canal of *Mustelus canis* (from S. E. Johnson, *J. Comp. Neurology*, 1917). *Can*, Canal wall ; *Clm*, columnar supporting cell ; *Fbn*, terminal fibrillae ; *Fb.Zn*, longitudinal fibre-zone ; *M.N.F*, medullated nerve-fibre ; *Sn.Cl*, secondary sense cell ; *Spn*, spindle-shaped supporting cell ; *Vas*, blood-cell.

contain not true sensory cells, but specialised gland cells which on stimulation secrete a substance acting on the afferent nerve-endings.

Acustico-lateral System.—The acustico-lateral or neuromast system is of peculiar interest. It is present in all Craniates from Cyclostomes to Man, and is found in the earliest fossil fish of the Silurian. While typically

developed only in aquatic forms, it survives in others as the inner ear ; for it becomes differentiated into two parts : (1) the neuromasts of the lateral-line system proper, and related superficial organs, and (2) the auditory labyrinth and its contained sensory organs. The first is stimulated by slow vibrations of the watery environment, and serves for the orientation of the body in relation to waves and currents (Séde de Lièoux, 1884 ; Parker, 1160). The second has two distinct functions—equilibrium in space or balance, and hearing. The semicircular canals of the labyrinth are chiefly concerned with balance, while vibrations of high frequency (sound-waves) affect the sensory cells in the sacculus and lagena of lower forms
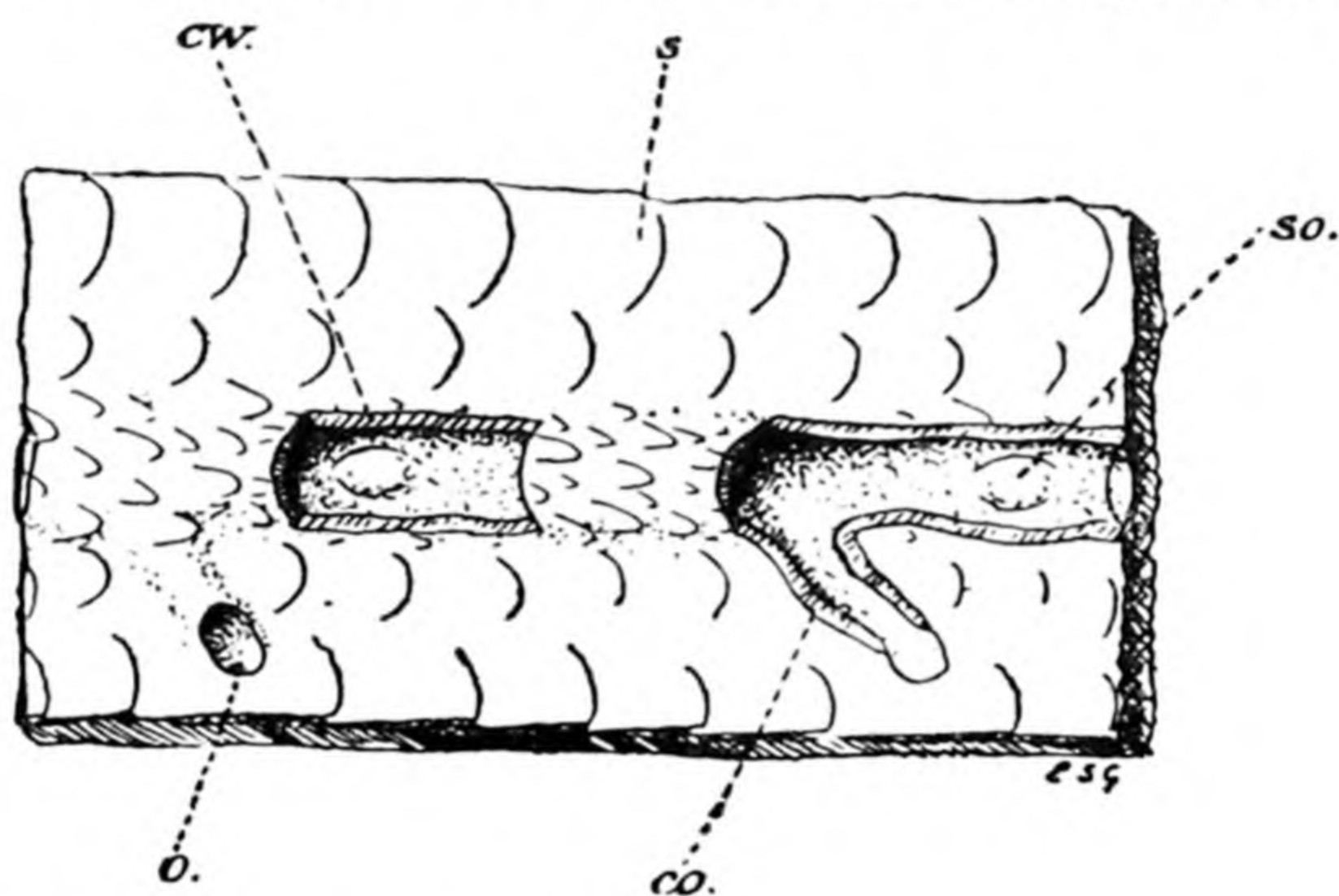
FIG. 714.

Gadus morrhua, L. Surface view of the skin, enlarged, showing the lateral line. *co*, Cut wall of canal to opening ; *cw*, cut wall of main canal ; *o*, opening ; *s*, scale ; *so*, sense organ (neuromast). (From Goodrich, *Vert. Craniata*, 1909.)

and the spirally coiled cochlea of Mammalia. The view that the sense organs of the internal ear are specialised deeply sunk neuromasts was put forth by Beard (1088) and Ayers (1086). It is supported by much weighty evidence, though no sufficiently primitive Craniate is yet known to show intermediate steps between the two kinds of organ. They both develop from similar dorso-lateral placodes (p. 765), both have sense cells pro-vided with sensory hairs receiving stimuli from a liquid medium (water or endolymph), both tend to sink away from the surface, and both are innervated by fibres from corresponding and related centres in the brain.

The special organs of the lateral-line system proper, neuromasts of Wright (1186), are distributed over the body, typically along lines forming a definite pattern on the head and extending along each side of the body to the tip of the tail. The neuromasts of Cyclostomes are exposed on the surface, but in primitive Gnathostomes they are usually sunk in a closed canal embedded in the dermis and opening at intervals by tubes to the

exterior (Leydig, 1851–68 ; Allis, 402 ; Herrick, 1121). As a rule the tube opens into the canal between successive neuromasts in Selachians and opposite them in Teleostomes, Figs. 712-15. Sometimes the primary external pores become subdivided into secondary pores, as in *Amia*, *Lepidosteus*, and some Teleosts (Allis, 402, 404-5). In *Chlamydoselachus*, however, the main line of the trunk is in the form of an open groove, Fig. 27 (Garman, 1111) ; also in *Chimaera*, where the edges of the groove do not
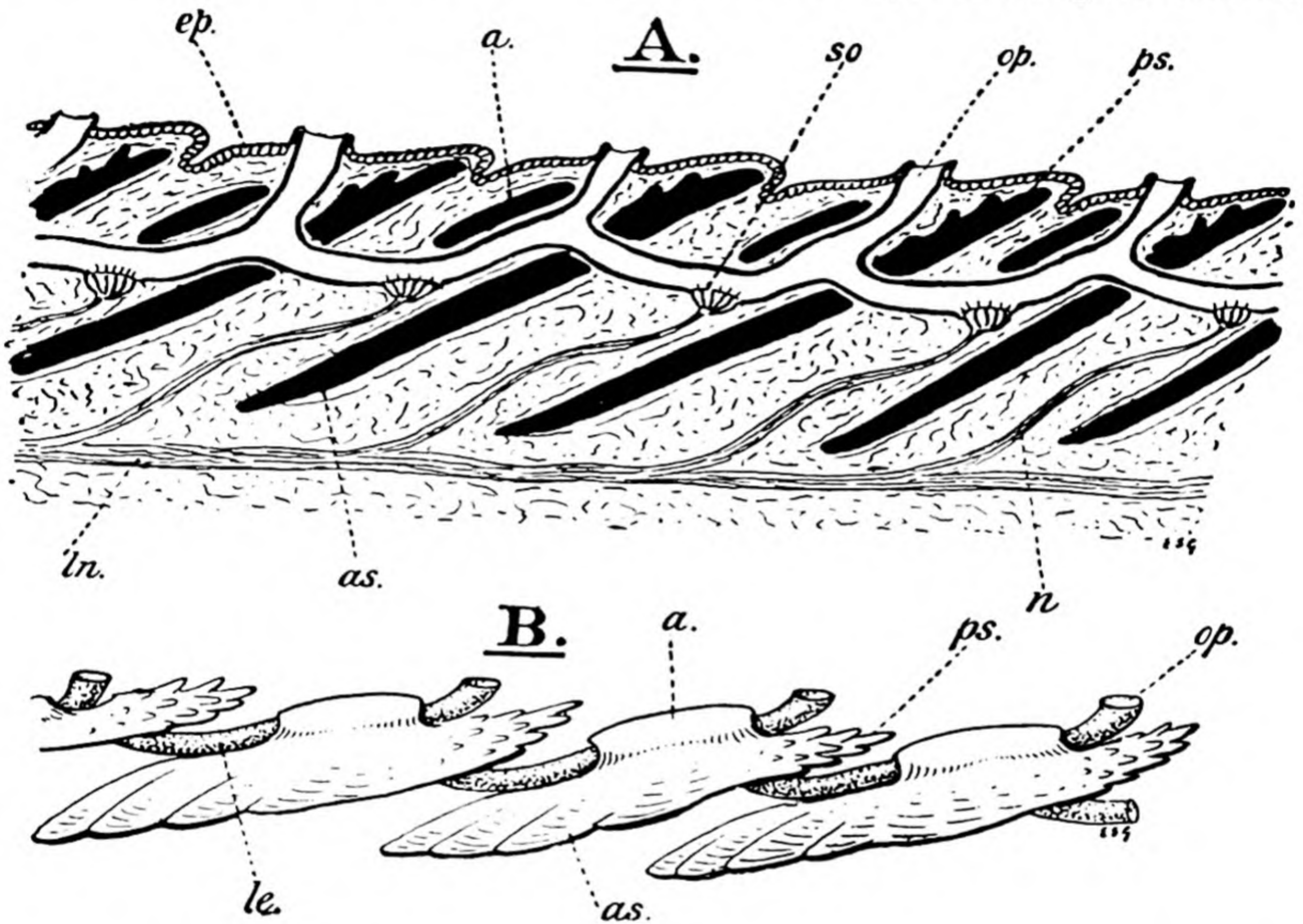
FIG. 715.

Diagrams showing the relation of the lateral-line canal to the scales on the trunk of *Perca fluviatilis*, L. A, Longitudinal section ; B, the scales and the canal seen from the side. *a*, Arch covering the canal ; *as*, anterior region of scale ; *ep*, epidermis ; *lc*, lateral-line canal ; *ln*, lateral-line nerve ; *n*, nerve to sense organ ; *op*, external opening of canal ; *ps*, posterior ctenoid edge of scale ; *so*, sense organ in canal. (From Goodrich, *Vert. Craniata*, 1909.)

completely close even on the head. Many of the more specialised Teleosts, and all modern aquatic Amphibia (Urodela and larval Anura and Apoda), have the neuromasts naked on the surface ; likewise the Dipnoi except on the head. This condition is no doubt secondary, at all events in Osteichthyes, for canals are found in their early fossil representatives, and even in Ostracodermi of the Silurian.

In the canals on the head the neuromasts may vary greatly in number, but along the main trunk line they are usually segmentally disposed in Pisces. Now, in the Osteichthyes, where bony dermal plates are developed on the head and shoulder girdle, and scales on the remainder of the body,

the canals enclosing the neuromasts necessarily become more or less completely enclosed in these plates and scales, Fig. 715. There is thus established a definite relation between the lateral-line system and the exoskeleton (p. 285). In all primitive Osteichthyes, the main lateral-line canal of the body pierces every scale along its course, passing from its upper surface in front to its lower surface behind. A neuromast is placed between each pair of scales, and a tube leads to a pore outside each scale. The same structure may be seen in the secondary longitudinal lateral lines often developed dorsally and ventrally as branches of the main line. Anteriorly the main line passes forwards through the dorsal elements of the shoulder girdle (post-temporal, etc.) on to the head.
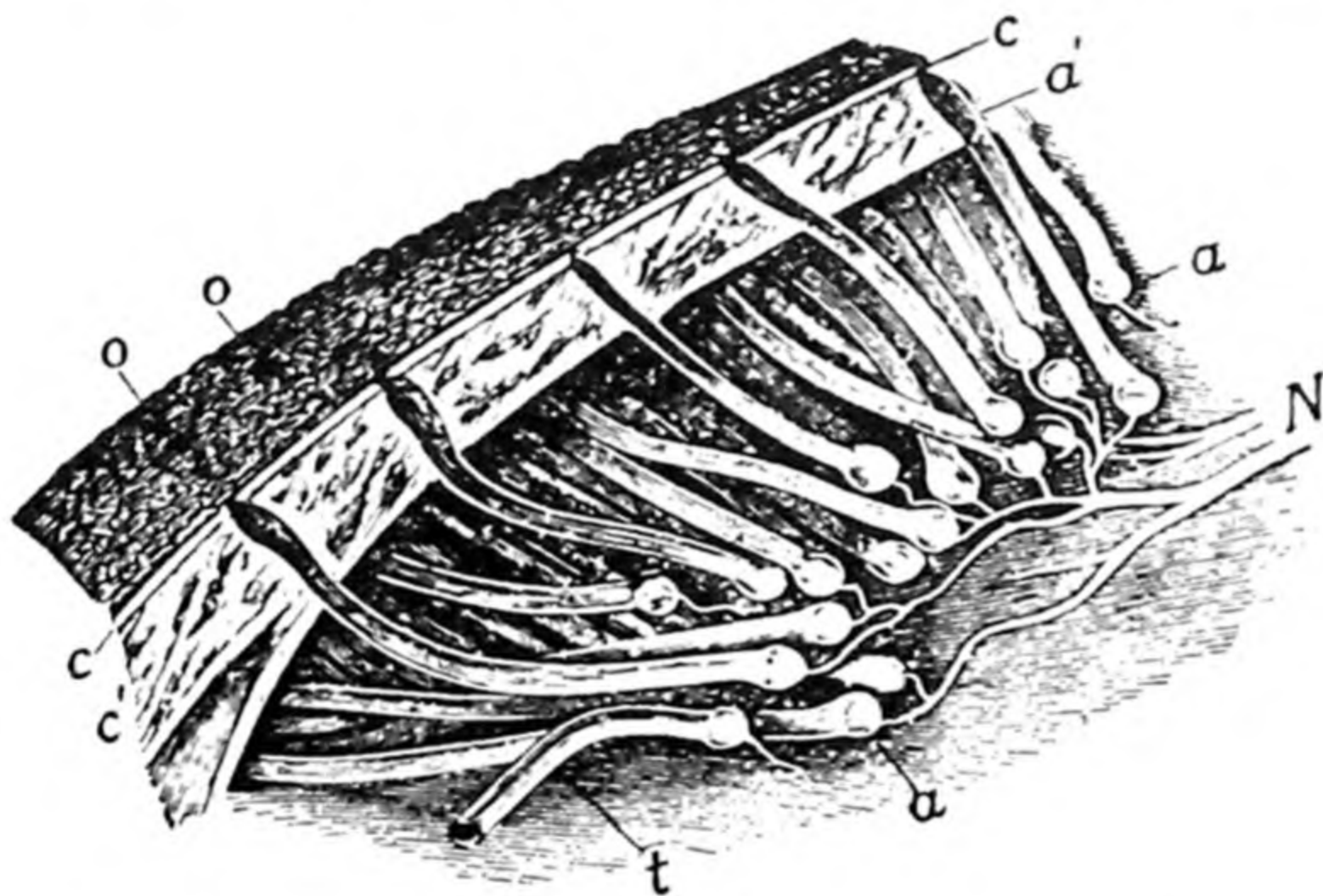
FIG. 716.

Portion of the snout of *Scyllium* in section, showing ampullary tubes. (After Gegenbaur, from Sedgwick's *Zoology*.) *a*, Ampulla; *a'*, passage of a tube through the dermis; *c*, epidermis; *c'*, dermis; *N*, nerve; *o*, external openings of tubes; *t*, tube.

This burial of the canals in the superficial skeleton occurs not only in the earliest Teleostomes and Dipnoi, but also in the Palaeozoic Ostracodermi (Pteraspidomorphi, Cephalaspidomorphi, Pterichthyomorphi) and Coccosteomorphi. In the Stegocephalia it was apparently less complete, as the course of the canals in these extinct Amphibia is at most marked by superficial grooves on the skull, Fig. 321. When, as in the later more specialised forms (Dipnoi, modern Amphibia, and many Teleostei), the dermal bones tend to sink far below the skin, the canals become again free in the superficial dermis, or, as already mentioned, the neuromasts come to lie naked on the surface.

There are present in Pisces other surface sense organs besides typical neuromasts; pit-organs, ampullae, vesicles, nerve sacs. As Herrick (1903) and Johnston (1129) have shown, all these organs belong to the acustico-lateral system, have essentially the same structure as neuromasts,

are innervated by the same component as the lateral-line organs, and are connected with the same centres in the brain, Figs. 717-18, 720.

Pit-organs generally appear in Selachians scattered or in rows on the dorsal surface of the head, along the hyoid arch, and dorsally along a line extending from the head backwards along the trunk (Allis, **412**; Norris and Hughes, **1158**). Teleostomes have more or less complete lines of pit-organs in approximately the same positions (Herrick, **1120**; Allis, **1081**). They are well developed in *Amia* and occur in addition on the cheek, mandible, and median gular. Lines on the cranial bones of fossil Dipnoi and Teleostomes seem to indicate their pre-
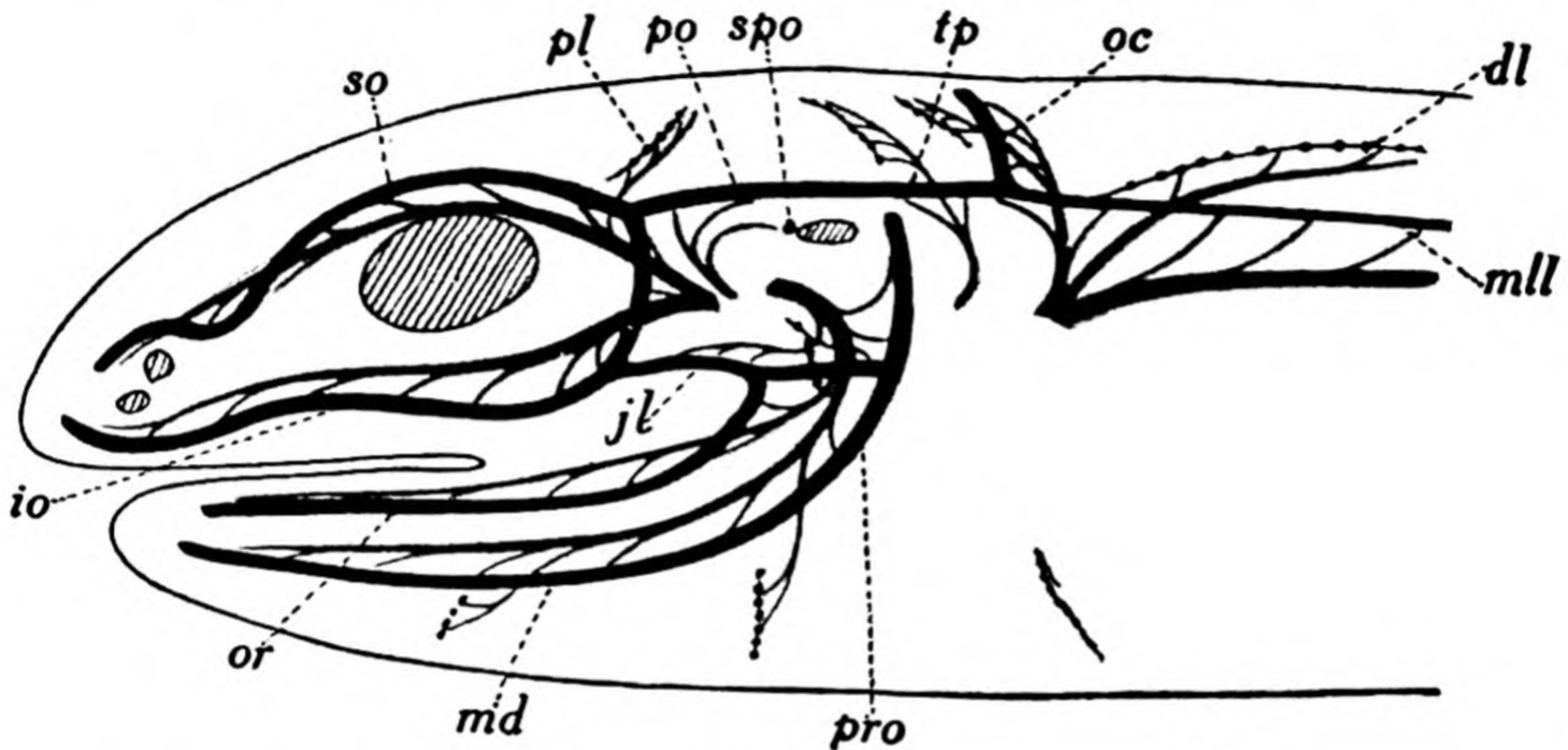
FIG. 717.

Left-side view of head of generalised Fish showing distribution of *lateral-line organs* and canals (black), and their *nerve-supply* (grey). *dl*, Dorsal line of pit-organs; *io*, infraorbital canal; *jl*, jugal canal; *md*, mandibular canal; *mll*, main canal of trunk; *oc*, transverse occipital canal; *or*, oral canal; *pl*, anterior of three lines of pit-organs—similar lines occur ventrally; *po*, post-orbital canal; *pro*, preopercular or hyomandibular canal; *so*, supraorbital canal; *spo*, spiracular neuromast; *tp*, temporal canal. For nerve-supply see Figs. 720 and 728.

sence in early forms. Sometimes these lines of neuromasts sunk in separate pits appear to represent in one form a true lateral-line canal in another.

The ampullae of Lorenzini of Selachians and Holocephali, on the other hand, are more specialised neuromasts sunk far below the surface in groups, above and below the snout, on the upper and lower jaws, and on the hyoid arch, Figs. 716, 718. A long tube leads from the swollen base of each to the external pore, which marks the point at which the organ was first developed (Sappey, 1880; Allis, 1082a). Doubtless the vesicles of Savi found in *Torpedo* are similar organs which have become separated off from the epidermis.

No ampullae occur in Osteichthyes; but Herrick (1903) has described, besides the lateral-line neuromasts and pit-organs, a third set of small

pit organs ' scattered over the body of Siluroids, and ' nerve-sacs ' are
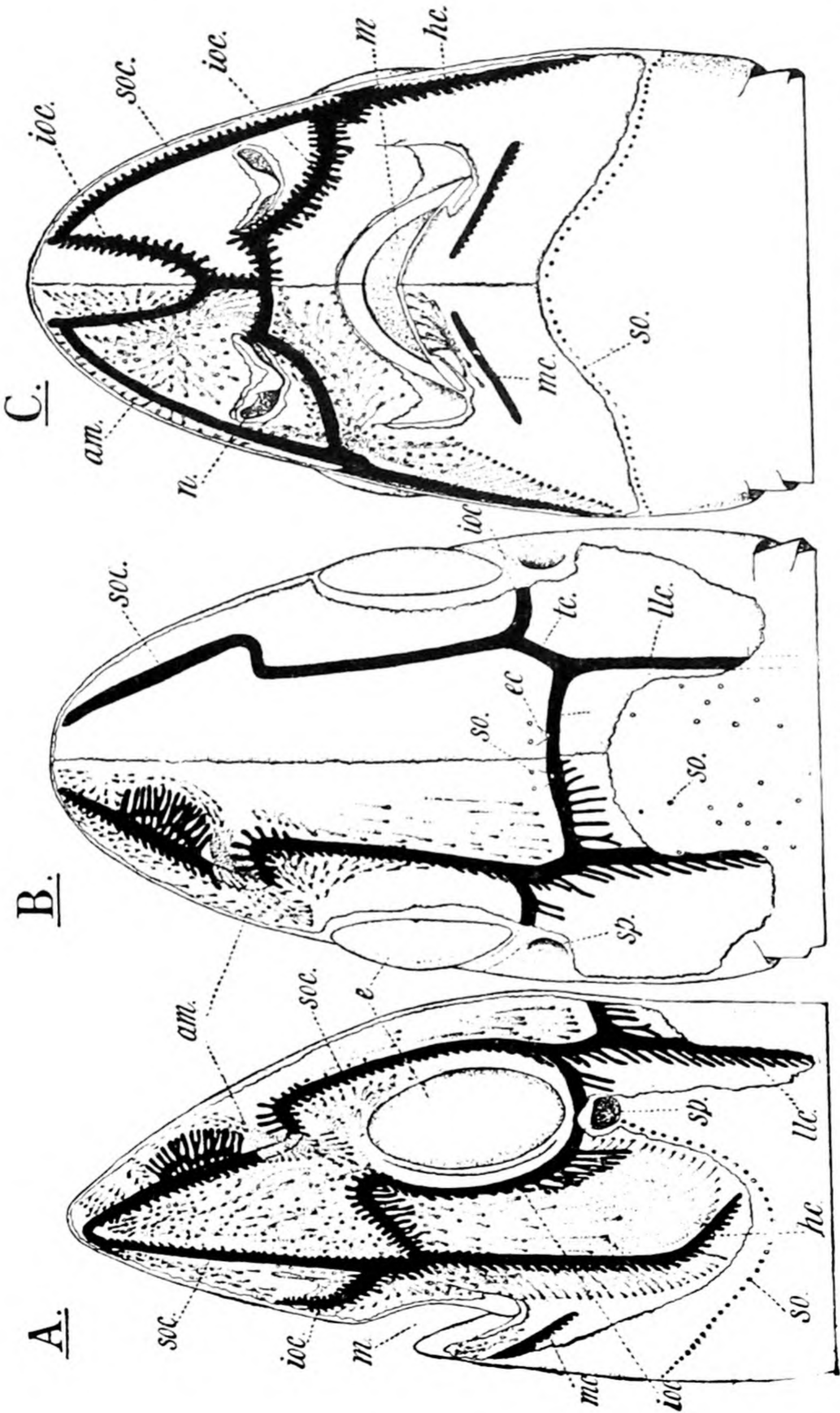
FIG. 718.

Mustelus laevis, Risso. A, side view, B, dorsal view, and C, ventral view, of the head, showing the course of the lateral-line canals, and the distribution of the ampullae (shown on the left side only). *Am*, Ampullae of Lorenzini ; *e*, eye ; *ec*, endolymphatic canal opening to the exterior ; *hc*, hyomandibular canal ; *ioc*, infraorbital canal ; *llc*, lateral-line canal of the trunk ; *m*, mouth ; *mc*, mandibular canal ; *n*, nostril ; *so*, sense-organ ; *soc*, supraorbital canal ; *sp*, spiracle ; *tc*, postorbital canal. (After Allis, from Goodrich, *Vert. Craniata*, 1909).

found below the skin in some forms. These may represent the ampullae of Selachians.

A complex pattern is formed by the lateral-line system on the head, remarkably constant, except for minor modifications, throughout the Gnathostomes. It is subdivided into regions innervated by the facial, glossopharyngeal, and vagus nerves by means of which three nerves (leaving aside the auditory) the fibres of this component are distributed not only over the head, but over the rest of the body as well. The course
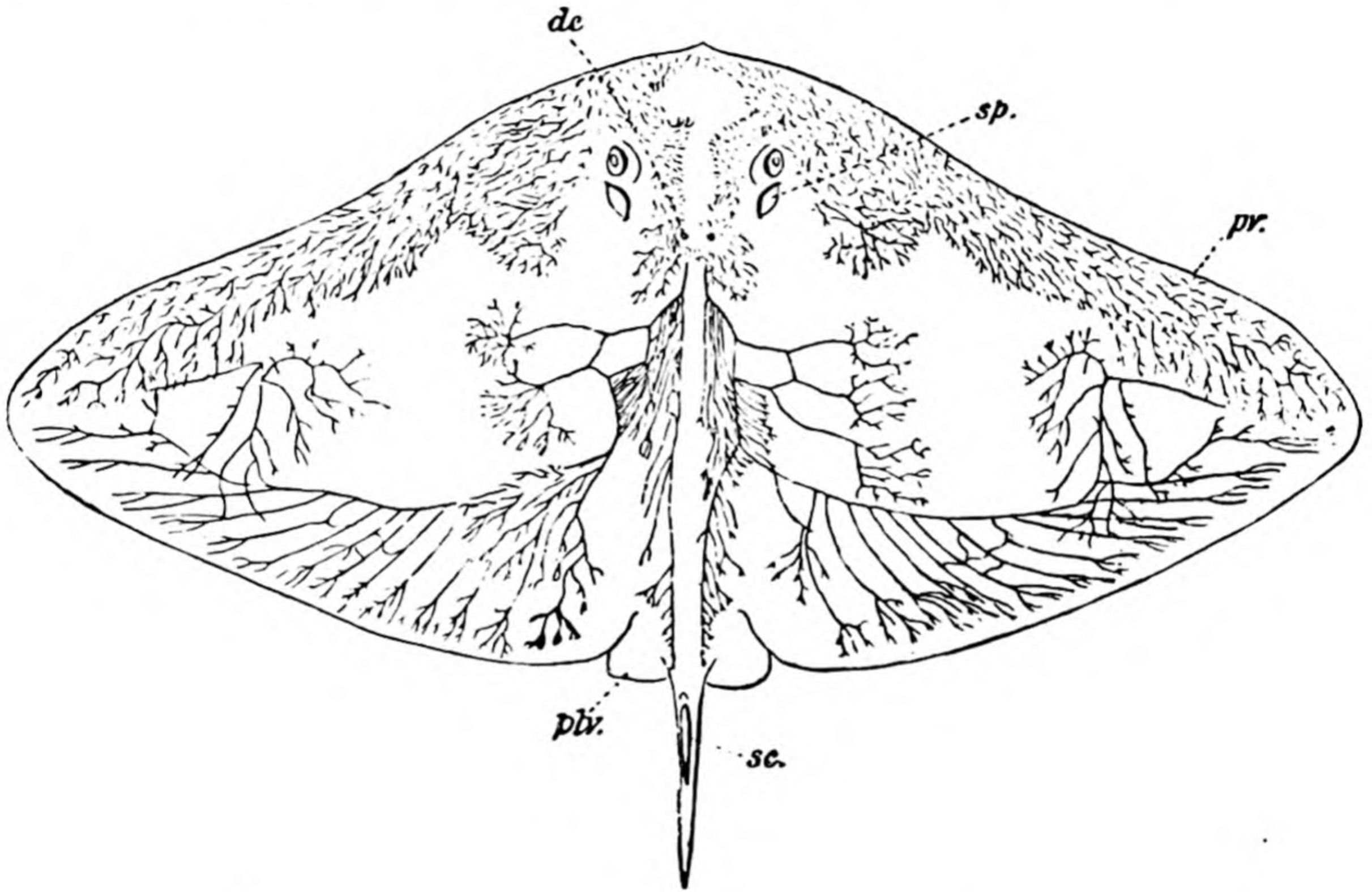
FIG. 719.

Dorsal view of *Pteroplatea Valenciennii*, Dum. (after Garman), showing the extensive development of the lateral-line organs. *de*, endolymphatic openings; *pv*, pectoral fin; *plv*, pelvic fin; *sc*, spine; *sp*, spiracle. (From Goodrich, *Vert. Craniata*, 1909.)

and nerve-supply of the canals or lines have been admirably described by many authors, among whom may be specially mentioned the works of Ewart on Selachians, Allis on *Amia*, and Herrick on *Menidia*. (Canals and innervation: Ewart and Mitchell, 1107, Allis, 1082a, Norris and Hughes, 1158, on Selachians; Cole, 1099, on *Chimaera*; Norris and Collinge, 476, on Chondrostei and *Lepidosteus*; Pollard, 575, Allis, 1082, on *Polypterus*; Herrick, 1120, Pollard, 1164, Cole, 1099a, Guitel, 1891, Allis, 404-5, in Teleostei; Pinkus, 1161, in Dipnoi; Strong, 1176, Coghill, 1098, Norris, 1155, Escher, 1106, in Amphibia. Courses of lateral line: Sappey, 1880, Garman, 1111, Reese, 1167, in Elasmobranchs; Collinge, 477-8, Goodrich, 35, 518, Stensiö, 218, 606, Watson, 646, in fossil Teleo-

stomes ; Malbranc, 1146, in Amphibia ; Moodie, 548-50, in Stegocephalia, Figs. 717-21, 725.

It will be readily seen from the figures that the general plan in Pisces is for the main canal or line of the trunk to run forward on to the head where it is continued to near the orbit. Here it divides one branch running above and the other below the eye to the snout. A canal may run across the cheek, and be continued along the lower jaw ; while another runs down the hyoid arch, and below the lower jaw. A dorsal
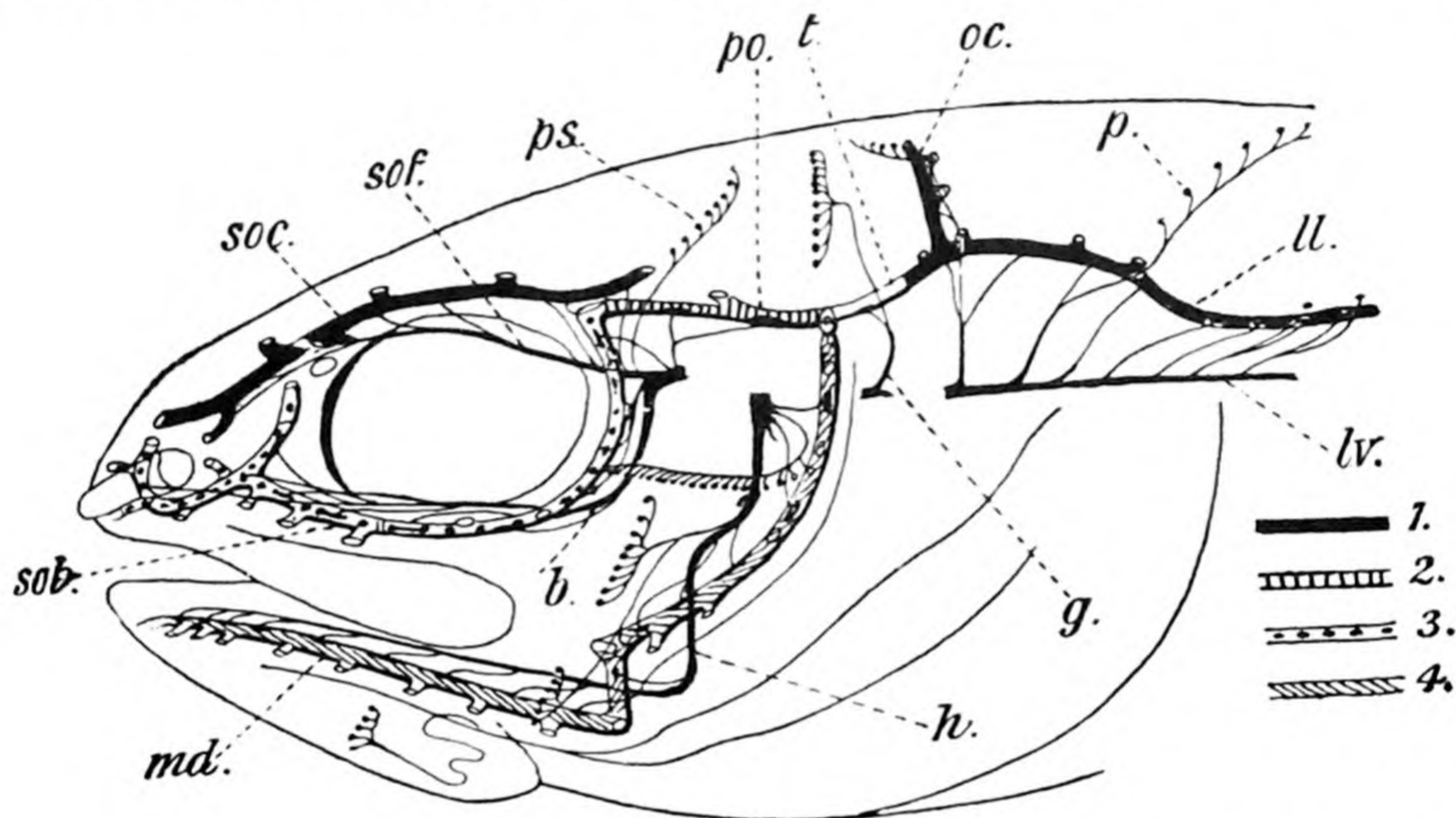
FIG. 720.

Diagram of the head of *Amia calva*, L., showing the system of lateral-line canals and pit-organs, and their nerve-supply (from Allis). *b*, Buccal branch of facial nerve ; *g*, dorsal branch of glossopharyngeal ; *h*, hyomandibular branch of facial ; *ll*, lateral line of trunk ; *lv*, lateral-line branch of vagus ; *md*, mandibular canal ; *oc*, occipital or supratemporal canal ; *p*, pit-organs on trunk ; *po*, postorbital canal ; *ps*, pit-organs on head ; *sob*, suborbital canal ; *soc*, supraorbital canal ; *sof*, superior ophthalmic branch of facial ; *t*, temporal canal. The system of distinguishing the canals is indicated on the right of the figure ; 1, supraorbital, and main canal of trunk ; 2, postorbital ; 3, suborbital ; 4, hyomandibular. (From Goodrich, *Vert. Craniata*, 1909.)

branch runs up across the occipital region. The chief parts of the head system have received names, the transverse occipital being known as the supratemporal, the horizontal and suborbital as the infraorbital, the part running above the orbit as the supraorbital, and the ventral branch as the hyomandibular, its continuation on the lower jaw being sometimes called the mandibular (in Osteichthyes these are often named preopercular and mandibular). But a more satisfactory nomenclature can be given, taking the nerve supply into account. The supraorbital line is supplied by the superior ophthalmic branch of the facial nerve ; the infraorbital by its buccal branch ; the hyomandibular and mandibular by the truncus hyomandibularis of the facial ; the jugal and oral by branches of the latter nerve ; the transverse occipital by the ramus supratemporalis of the

vagus. There remains the horizontal line from the orbit to the main line of the trunk. This region is generally included in the 'infraorbital'; but, since between the anterior part supplied by the otic branch of the facial and the beginning of the main canal there is generally intercalated a short region innervated by the supratemporal branch of the glossopharyngeal, it would seem better to name these two horizontal regions the postorbital and temporal respectively (Goodrich, 35) as indicated in
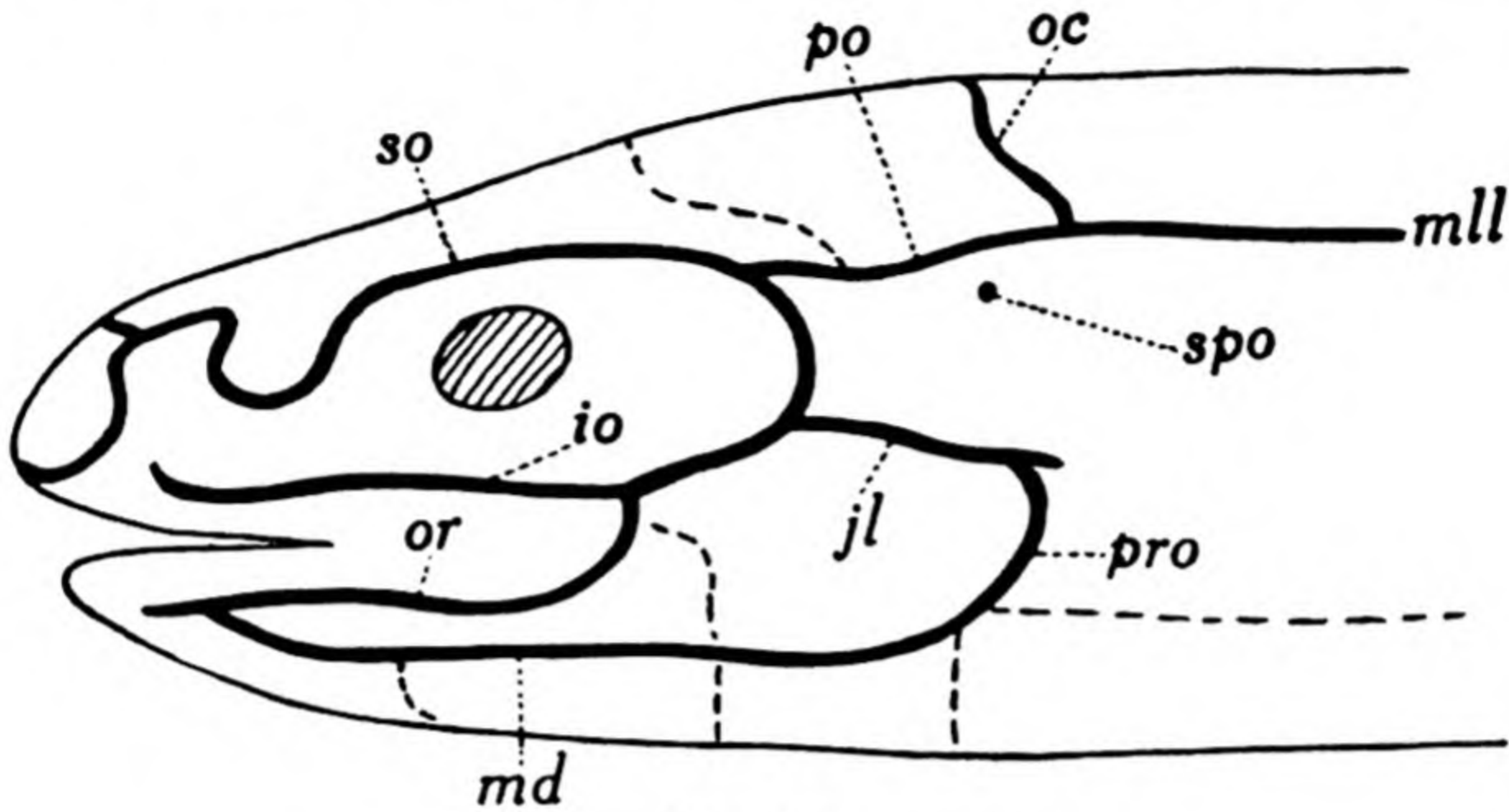
FIG. 721.

Diagram of lateral-line system of *Dipnoi*; canals thick black lines; pit organs broken lines. Lettering as in Fig. 717.

Figs. 717, 720.[1] The main line of the trunk is innervated by the ramus lateralis of the vagus.

Specialisation in various groups may lead to the interruption, subdivision, branching, and fusion of these primary lines.

The supraorbital canal of Selachians becomes much developed on the rostrum, and joins the infraorbital, which may pass forward between the mouth and the nostril (*Squalus, Mustelus*). A transverse commissure may be formed by the junction of the right and left occipital canals, while the hyomandibular fails to meet the postorbital but runs forward longitudinally (jugal canal) to join the infraorbital, the mandibular being separate. Missing parts of the hyomandibular canal seem to be represented by pit-organs.

The occipital transverse commissure is usually completed in Osteichthyes across the middle line. While in Actinopterygii, even in the fossil Palaeoniscoidei (Stensiö, 218; Watson, 646), the hyomandibular canal joins the postorbital dorsally, and does not run across the cheek to the infraorbital (being represented here by pit-organs in *Amia*, Allis, 1081). In Dipnoi, Osteolepidoti, and Coelacanthini (Stensiö, 605-6; Goodrich,

[1] The temporal canal is often very short and sometimes eliminated by the backward extension of the postorbital line, as in *Menidia* (Herrick, 1120).

518-19; Watson 644) there is usually a jugal canal across the cheek as in Selachians, Figs. 721-4.

The distribution of the neuromasts in modern Amphibia (Malbranc, 1146; Kingsbury, 1133; Escher, 1106) agrees in general with that of primitive fishes and is remarkably like that of Dipnoi.[1] The lateral-line grooves on the skull of Stegocephalia often clearly show the jugal connexion of the hyomandibular canal with the infraorbital mentioned above, Fig. 725 (Moodie 548-50).

On the other hand, the Cyclostomes differ considerably from the Gnathostomes in the pattern of the lateral-line system, which always remains superficial (Alcock, 1080; Johnston, 1128; Stensiö, 1926). It is better developed in Petromyzontia than in Myxinoidea, where it was discovered by Ayers and Worthington (1087).

In *Petromyzon* there is a main line running down the side of the body to the end of the tail, and a more dorsal line above. These pass forwards above the gill openings to the hind region of the head. The main line reaches to the orbit and another line extends beyond

FIG. 722.

Dorsal view of head of *Ceratodus forsteri*, showing lateral line canals seen through skin and over-lying scales. *ac*, Anterior commissural; *ioc*, infraorbital; *jl*, jugal; *ll*, main trunk; *oc*, transverse occipital; *orc*, oral; *r*, rostral, *soc*, supraorbital, and *tc*, temporal canals; *l*, eye.

it; the former represents the postorbital and the latter probably the infraorbital canal. Further forward still is a line representing the supraorbital. Two dorsal transverse lines, one just behind the orbit and the other further back, may represent the dorsal pit-organs and occipital lines of Gnathostomes. A line runs round each side of the oral sucker, and from these extend two longitudinal ventral lines along the gill region. There are also groups of neuromasts between each pair of gill-slits, and

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[1] The lateral-line organs and their nerves are eliminated in those Amphibia which adopt a permanent terrestrial life; but persist in those Urodela which retain the aquatic habit, and also, among Anura, in the aquatic Aglossa, and partially in *Bombinator* (Escher, 1106).

between the ventral lines are groups or short transverse lines corresponding to each gill opening. All these neuromasts appear to be innervated by branches of 7th, 9th, and 10th cranial nerves as usual. Stensiö (1926) has recently pointed out that the pattern of the lateral-line canals, first recognised by Lankester in the Pteraspidomorphi, closely resembles that of the lines of neuromasts in modern Cyclostomes; an important piece of evidence in favour of the view advocated by Cope, Woodward, and Stensiö, that these two groups are related. The lateral-line organs of the Pteraspidae are, however, in canals deeply embedded in the bony shields (A. S. Woodward, 663; Goodrich, 35).

Fig. 723.

Ventral view of head of *Ceratodus forsteri* showing course of lateral-line canals running below skin and scales. *an,* Anterior nostril; *ioc,* infraorbital, *jl,* jugal, *mdc,* mandibular, *orc,* oral, and *r,* rostral canals.

Whether the acustico-lateral system was originally segmented or not is an important question we may now consider. It is a striking fact that in all Craniata the whole system is innervated by cranial nerves. That the main lateral line extending to the tip of the tail is supplied by a branch of a cranial nerve, the vagus, requires explanation. Some authors, laying stress on the fact that in many Selachians and especially in Teleostomes the neuromasts of the main lateral line are strictly segmental, consider that this was their original disposition (Solger, 1879–82; Bodenstein, 1882; Hoffmann, 1883; Beard, 1088), and it has been suggested that the ramus lateralis vagi is a collector nerve (Eisig, 1887), presumably formed by the gathering forwards of all the posterior lateralis components of the spinals into the root of the vagus; a similar gathering of other components may account for the longitudinal branchial branch of the same cranial nerve (p. 767). Others, on the contrary, would consider that the acustico-lateral system was not originally segmental at all, belonged to the head region, stood as it were apart, and has only secondarily been included in and distributed by the 7th, 9th, and 10th cranial nerves. The majority of modern authors adopt a somewhat intermediate view (Strong, 1176; Herrick, 1120; Johnston, 1129, and others): that it is a special neuromast component differen-

tiated from the general visceral sensory system of these three cranial nerves which has secondarily extended backwards on to the trunk and tail. As evidence that the main line has phylogenetically grown
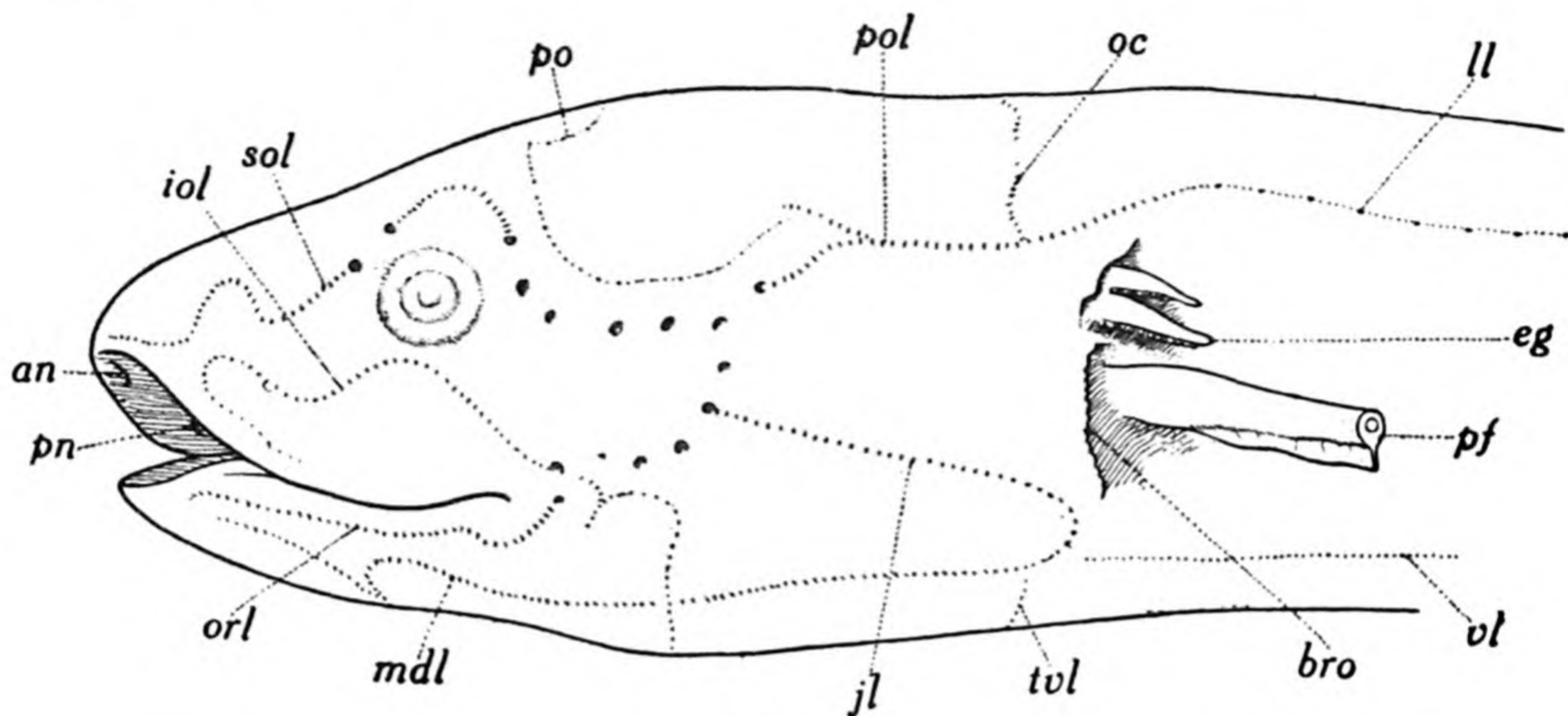
FIG. 724.

Protopterus annectens, left-side view of anterior region showing lateral line system ; pectoral fin cut short. *an*, Anterior nostril ; *bro*, branchial opening ; *eg*, external gill ; *iol*, infraorbital line ; *jl* jugular line ; *ll*, main line of trunk ; *mdl*, mandibular line ; *oc*, transverse occipital line ; *orl*, oral line ; *pf*, pectoral fin ; *po*, transverse postorbital line ; *pol*, postorbital line ; *pn*, posterior nostril ; *sol*, supraorbital line ; *tvl*, transverse ventral line ; *vl*, longitudinal ventro-lateral line.

backwards from the head it is pointed out that such invariably is its development in the embryo. For it is always derived from an ecto-dermal thickening or dorso-lateral placode, in the region of the vagus,
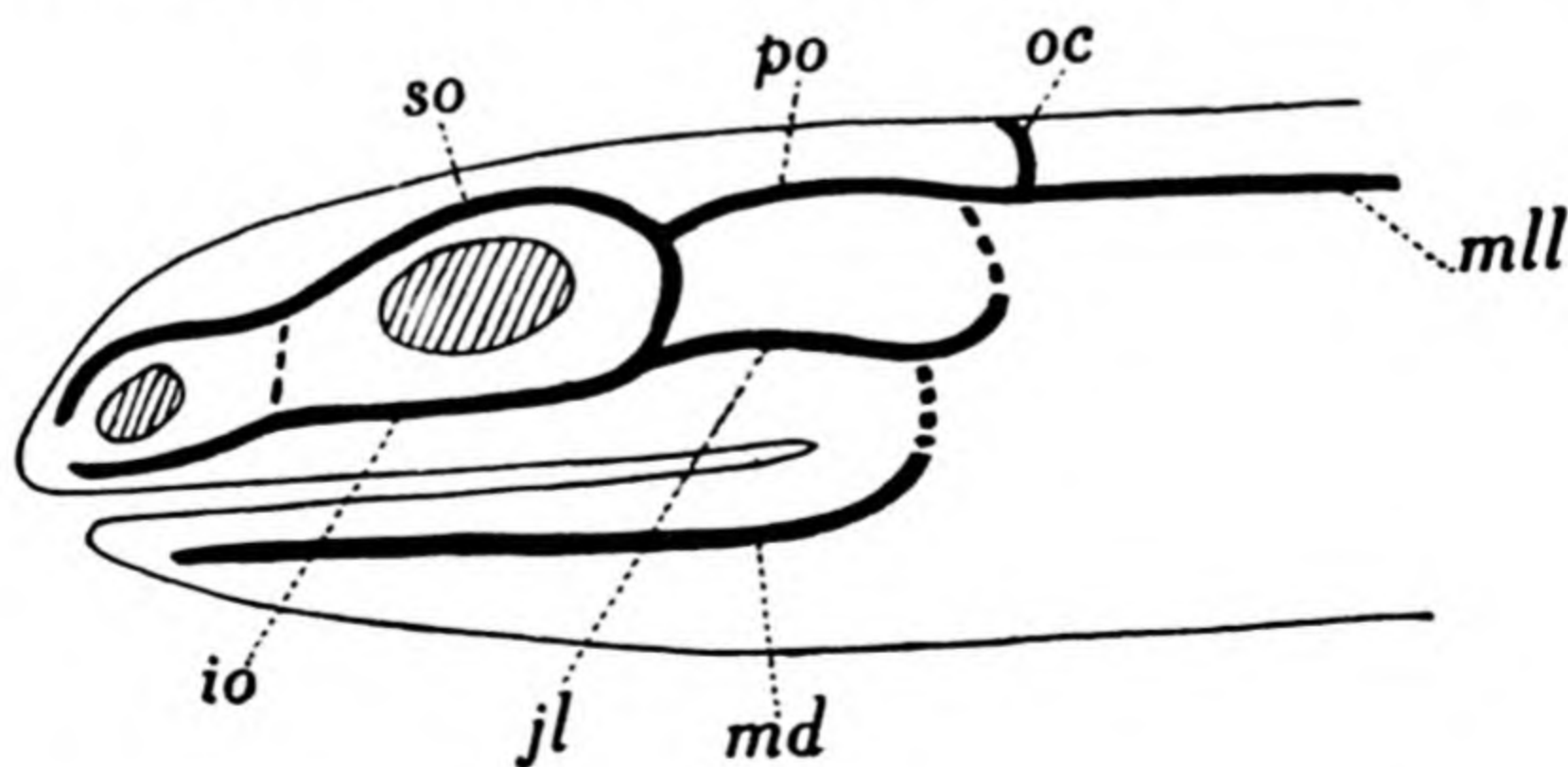
FIG. 725.

Diagram of lateral-line system in *Stegocephalia*.   Lettering as in Fig. 717.

which later extends over the trunk, growing at its tip and burrowing its way through the epidermis until it reaches the end of the tail (Balfour, 317 ; Dohrn, 1105 ; Johnston, 1129 ; Wilson, 1185 ; Allis, 1081). Harrison by an ingenious experiment has shown that, if the tail region of one tadpole be grafted on to the head of another, the lateral-line rudiment of the

latter will grow backwards on to the tail in a most independent manner (1903).[1]

Moreover the neuromasts are not segmentally arranged on the head of any known Craniate, and in some Selachians (*Mustelus*, Johnson, 1125a) they appear as an almost continuous line of sensory epithelium even along the main line.

On the other hand, certain facts seem to support the segmental theory. In most forms it has been found that the lateral-line system arises from a series of dorso-lateral placodes, at first independent (except perhaps in Teleostomes) and related to the 7th, 9th, and 10th cranial nerves (p. 765). In *Petromyzon* a lateralis component is associated with the profundus nerve, and in other aquatic Craniates lateralis fibres become associated with the ramus ophthalmicus superficialis and r. maxillaris of the trigeminal. These fibres are generally considered to belong to the facial nerve (r. of ophth. superf. facialis and r. buccalis), but they can be interpreted as a component of the trigeminal whose lateralis rootlet has secondarily joined that of the facial (Allis, 402).

Similarly with the metaotic segments, the vagus may have had a lateralis component in each of its segmental branchial branches. According to Alcock, indeed, the branchiomeric groups of neuromasts in the young Ammocaete are supplied by fibres passing down each gill arch (this important point has, however, not been confirmed by Johnston (1128)), the first two groups being supplied from the facial and glossopharyngeal. Also lateralis fibres to the ventral group of neuromasts near the yolk stalk of Selachians according to Norris and Hughes (1150), pass down the arch between the 4th and 5th gill-slit.

These observations all suggest that originally each head segment had its lateralis component, and that with increasing specialisation they became more and more concentrated into the facial, glossopharyngeal, and vagus segments, and in some cases survive only in the facial and vagus segments. This might be brought about by the collecting of the lateralis rootlets of the first two segments into the facial, and of the posterior body segments into the vagus. Further study of the system in Cyclostomes might throw light on this obscure subject.

The development of the lateral-line system has been described by many embryologists since Balfour (von Kupffer, 363, and Koltzoff, 361, in *Petromyzon*; Mitrophanow, 1148, Klinkhardt, 1134, Dohrn, 1105,

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[1] These observations and experiments are not quite conclusive. It may still be argued that the building material for the lateral line, although phylogenetically derived from successive body segments, has been in ontogeny precociously gathered near the root of the vagus and grows backwards later.

in Selachians ; Allis, 1081, in *Amia* ; Wilson, 1185, in Teleosts ; Platt, 1162, Mitrophanow, 1887, Brauer, 1094, Brachet, 993, in Amphibia). Good accounts have recently been given of the origin of the lateral-line system in Selachians by Johnson (1125a) and Ruud (1171). The ectoderm early becomes thickened over wide lateral and ventral regions on the head, and in these 'fields' appear special thickenings or placodes (p. 765), connected by strands with the underlying rudiments of the cranial ganglia. There can soon be distinguished supraorbital, infraorbital, and postorbital placodes in front of the auditory placode, and a row of post-auditory placodes overlying the glossopharyngeus and four branches of the vagus. The backward growth of the coalesced two posterior vagal placodes gives rise to the main lateral line of the trunk. The placode of the second vagal segment grows dorsally and caudally to form the more dorsal row of neuromasts, while that of the

FIG. 726.

Ventral and left-side views of anterior region of embryo of *Spinax niger*, showing rudiments of lateral line system (from G. Ruud, *Zool. Jahrb.*, 1920). *B*, Pectoral fin ; *dp*, dorsal trunk line ; *hmp*, mandibular line ; *io*, infraorbital line ; *K*, gills ; *l*, main trunk line ; *l**, transverse occipital line ; *M*, mouth ; *N* and *Na*, nasal organ ; *Ø*, orbit ; *so*, supraorbital line ; *Sp*, spiracle ; *stp*, temporal line.

first vagal segment forms the transverse occipital line. The glossopharyngeal placode contributes to the main line and dorsally gives rise to the supratemporal pit-organs. A ventral placode yields the pit-organs near the base of the pectoral fin, Figs. 726-7.

From the lengthened postorbital placode arises the postorbital line supplied by the otic branch of the facial. The infraorbital line is developed from the corresponding placode overlying the maxillary branch of the

trigeminal, and the hyomandibular line from a placode extending along the hyoid bar. The mandibular line appears in Torpedo to be developed from a separate placode related to the mandibular branch of the trigeminal. The exact history of the supraorbital line is not yet clear. In Selachians it appears to develop from a supraorbital placode at first related to the developing profundus ganglion. But in *Petromyzon* two placodes are described in this region, one at first connected with the profundus ganglion and the other with the facial. Eventually the supraorbital placodes give rise to the supraorbital line supplied by the r. ophthalmicus facialis, and the infraorbital placode to the line supplied by the r. buccalis facialis. These various lines grow in length, like the main line of the trunk, by multiplication of the cells at the tip, and burrow their way through the
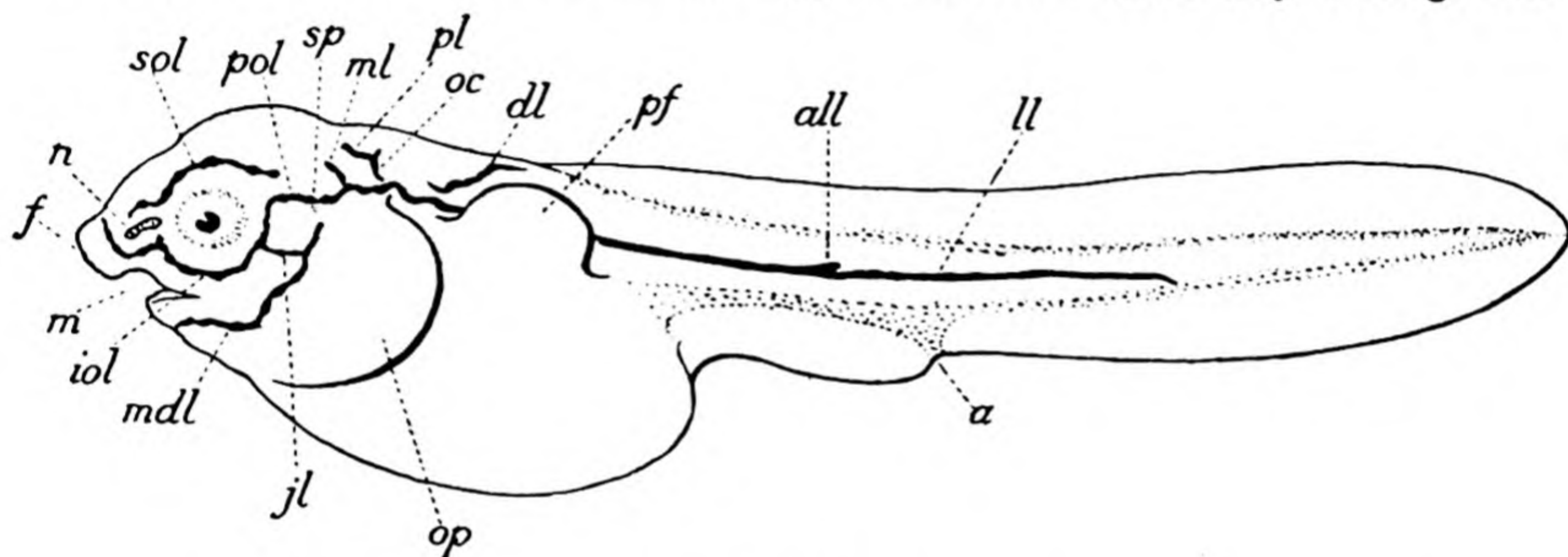
FIG. 727.

Larva of *Amia calva* (after Allis, 1889). *a*, Anus; *all*, accessory lateral line bud; *dl*, dorsal line of trunk; *iol*, infraorbital, *ll*, main trunk, *mdl*, mandibular, *oc*, occipital, *pol*, postorbital, *sol*, supraorbital lateral-line canal rudiments; *f*, fixing organ; *m*, mouth; *n*, undivided nasal opening; *jl*, *ml*, and *pl*, pit lines; *op*, opercular fold; *pf*, pectoral fin; *sp*, position of closed spiracle.

general ectoderm. *Amia* and Amphibia resemble very closely the Selachii in the distribution of placodes and development of the lateral lines, Fig. 727. In *Necturus*, however, the ventral neuromasts are more developed and the lines pass below all the gill-slits (Platt, 1162). The true relation of the rudiments of the lateral lines to the three preotic segments is still obscure. Although in the adult all the lines developed from them appear to be innervated from the facial nerve, yet at their first appearance placodes seem to belong to each of these three segments. This observation, together with that of an originally separate placode on the glossopharyngeal and each of the vagal segments, lend support to the view discussed above that the lateral-line system was originally distributed segmentally on the head.

General Cutaneous and other Components.—The history of the other components is easier to deal with, Fig. 728. It is clear that the general cutaneous was originally present in every segment of the body as it still

is in *Amphioxus* (Johnston, 1127). In the Craniate it is the dominant component in the first two segments of the head, the profundus being apparently composed of general cutaneous fibres only, and they are always abundant in the trigeminal. General cutaneous fibres are retained in all the other segments of Cyclostomes (*Petromyzon*, Johnston, 1128) ; but in Gnathostomes, although well represented in all the spinal nerves, this component tends to be reduced in the intermediate segments. The sensory area supplied by the profundus and trigeminal covers the greater part of the head and meets that supplied by the first complete spinal in Amniota, excepting for the area innervated by the r. auricularis of the vagus.

General visceral sensory fibres are probably present in every segment of the body in *Amphioxus*, except perhaps the first and last few. They are greatly developed in the 7th, 9th and 10th cranial nerves of Craniata. When present, as in Teleosts, in the maxillary and mandibular branches of the trigeminal, they are generally supposed to have been borrowed from the facial. This component is peculiarly well developed in the branchial region of Cyclostomes and Fishes.

The general occurrence and distribution of the components in the various groups of vertebrates may be gathered from Fig. 728.

Branchial and Spinal Nerve.—Before describing the cranial nerves the structure of a complete dorsal nerve of the branchial region of a fish may be explained and contrasted with that of a typical spinal nerve. A complete branchial nerve would have lateralis, general cutaneous, general visceral, special visceral, and visceral excito-motor rootlets, and a dorsal ganglion. The lateralis fibres would be given off as dorsal and lateral branches (ramus supratemporalis, etc.) ; the general cutaneous fibres as a dorsal branch (r. auricularis, etc.). The general visceral sensory fibres would pass inwards as a ramus pharyngeus, also containing special visceral fibres to taste-buds, and on either side of the gill-slit as pre- and post-trematic branches. Of these, the r. pretrematicus internus and externus are composed of visceral sensory fibres, as are the two external and one internal post-trematic rami. The visceral motor fibres pass down the r. post-trematicus posticus. Such a theoretically complete branchial nerve is rarely if ever found in fishes, since two or more branches may combine and some of the components may be absent (Sewertzoff, 1173 ; Allis, 404-5 ; Norris, 1156-7). Usually, however, there are three distinct branches, a visceral sensory pharyngeal, a visceral sensory pre-trematic, and a mixed visceral sensory and motor post-trematic ; there may also be a small dorsal general cutaneous branch and lateralis branches. Certain visceral sensory and excito-motor fibres may pass into ' sympathetic ' nerves. The somatic motor-root of the segment is, of course,

separate and contributes to the hypoglossal nerve in metaotic segments.

Cyclostome
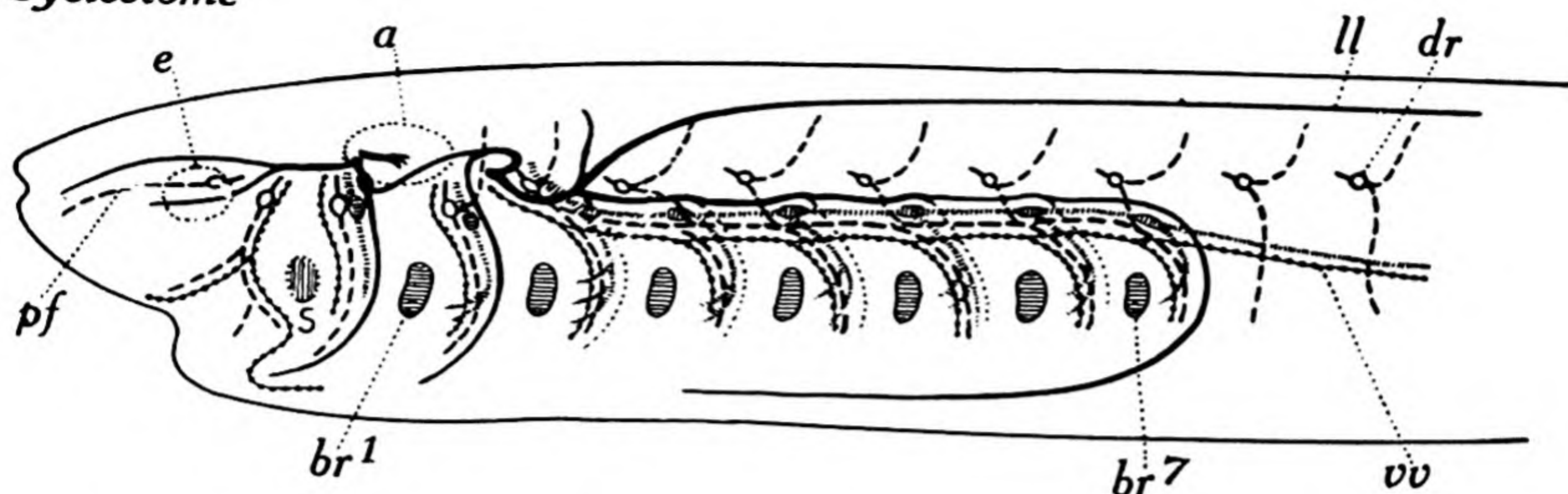
Selachian
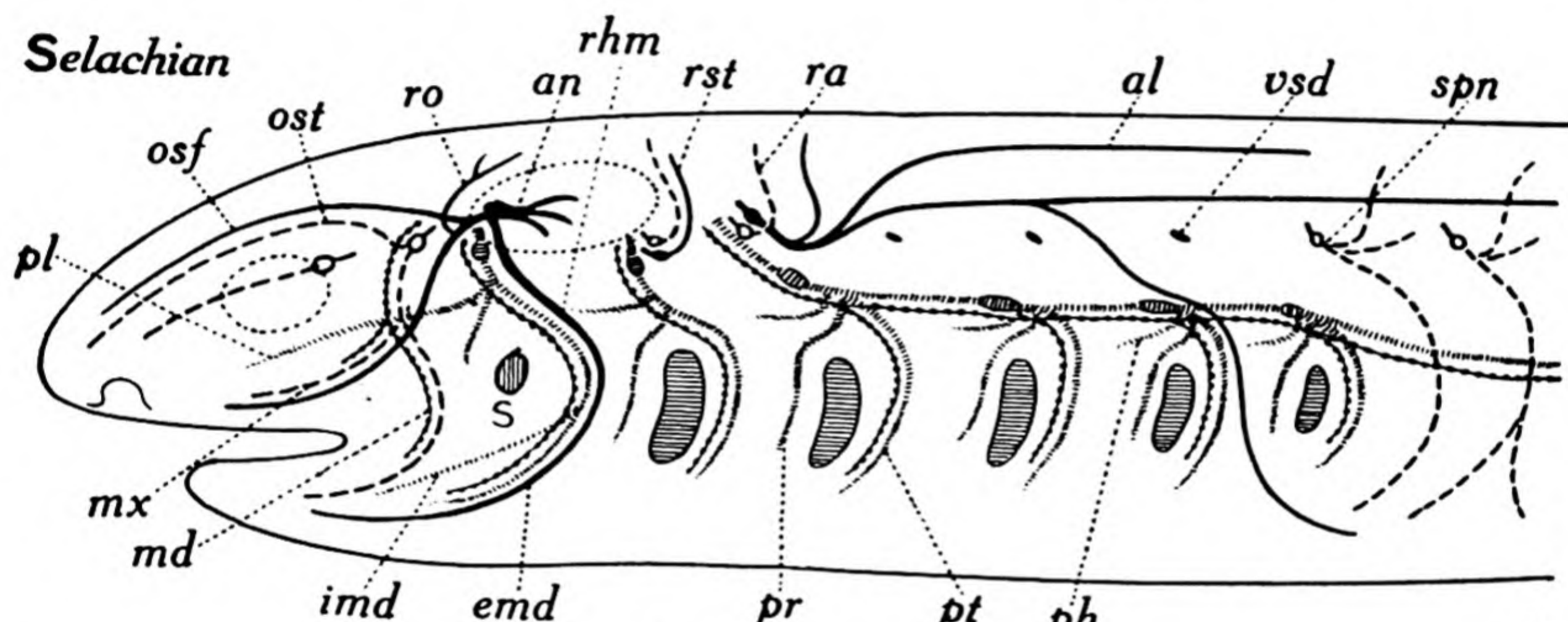
Teleost
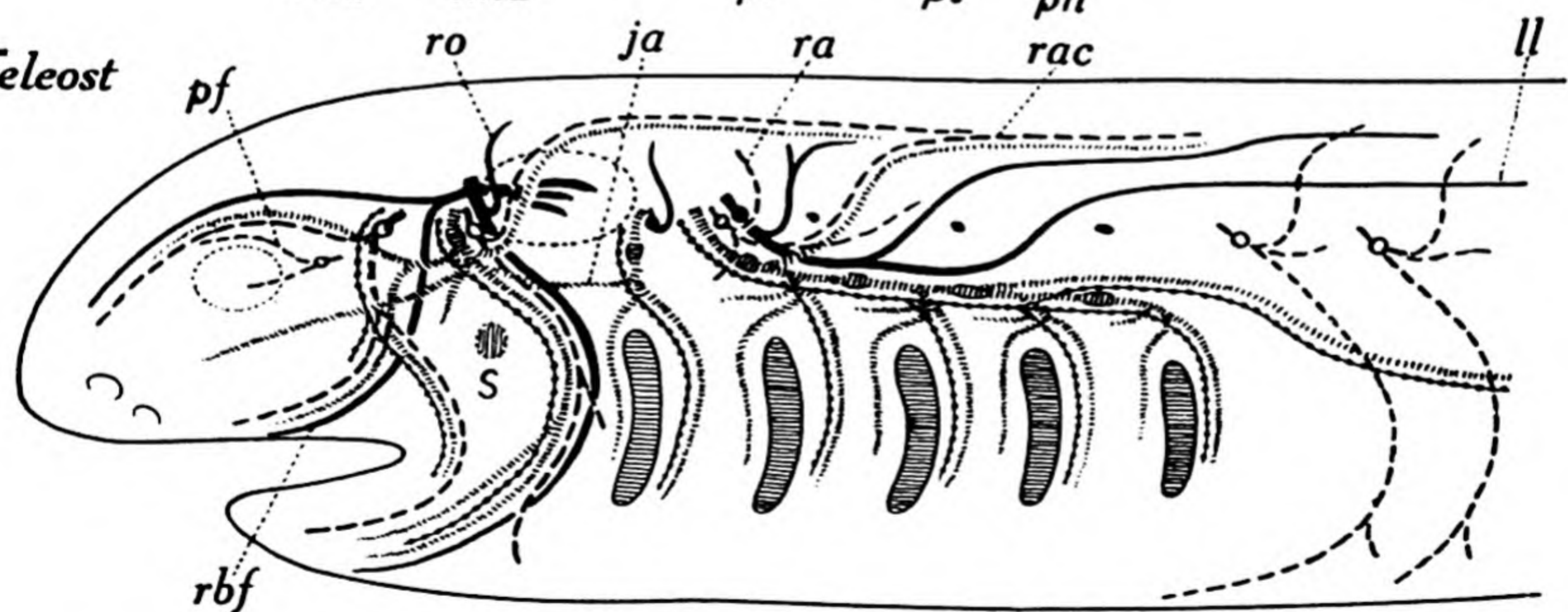
FIG. 728.

Diagrams of *Components* of dorsal root cranial nerves of *Gnathostomes*; ventral root nerves (somatic motor component) to eye-muscles and hypoglossal muscles omitted. *a*, Auditory capsule; *al*, accessory line; *an*, auditory nerve; *br*[1-7], branchial slits; *cht*, chorda tympani; *clbr*, closed branchial slit; *dr*, dorsal root nerve of trunk; *e*, eye; *emd*, external mandibular; *fa*, facial and auditory rootlets; *gl*, glossopharyngeal; *imd*, internal mandibular; *ja*, Jacobson's anastomosis; *ll*, main lateral line nerve; *md*, mandibular; *mx*, maxillary; *osf*, superior ophthalmic of facial;

A typical spinal nerve in a fish has a dorsal root chiefly of general cutaneous fibres and a ganglion; and this root joins a ventral root

chiefly of somatic motor fibres. The mixed nerve gives off a sensory anterior dorsal branch, and a motor posterior dorsal branch which joins

Aquatic Amphibian
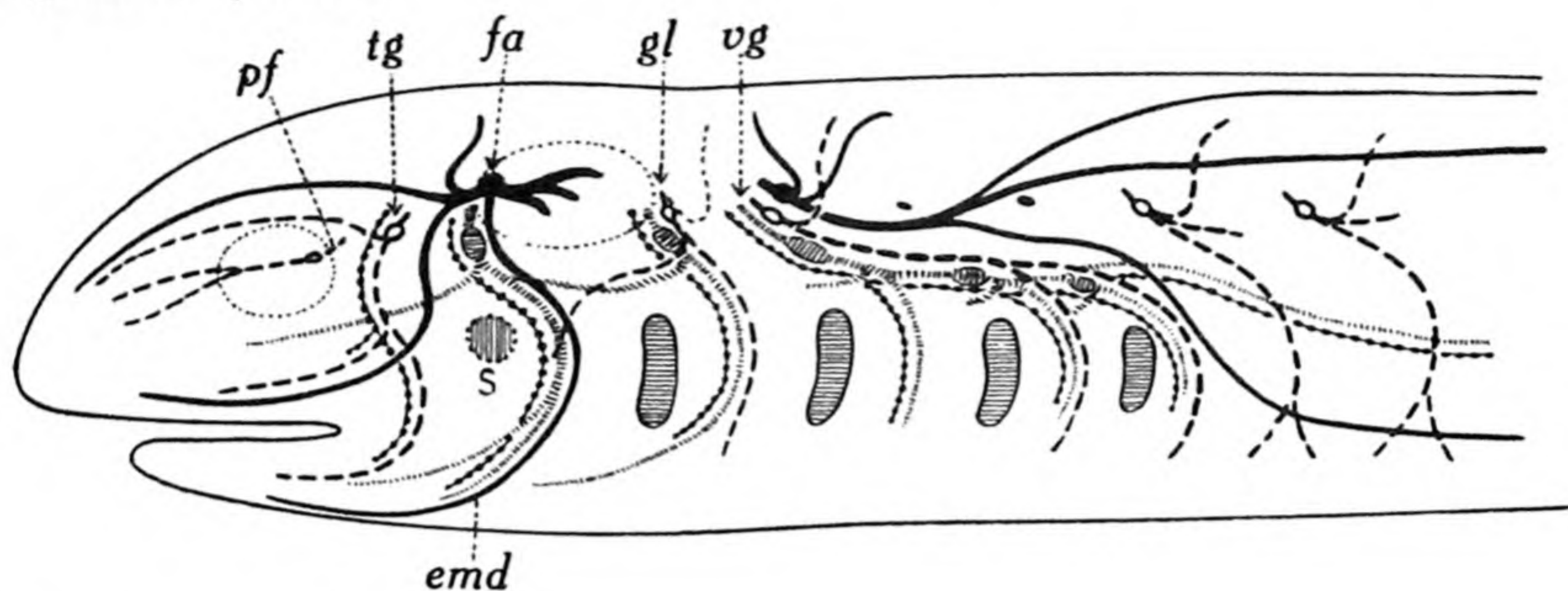
Terrestrial Amphibian
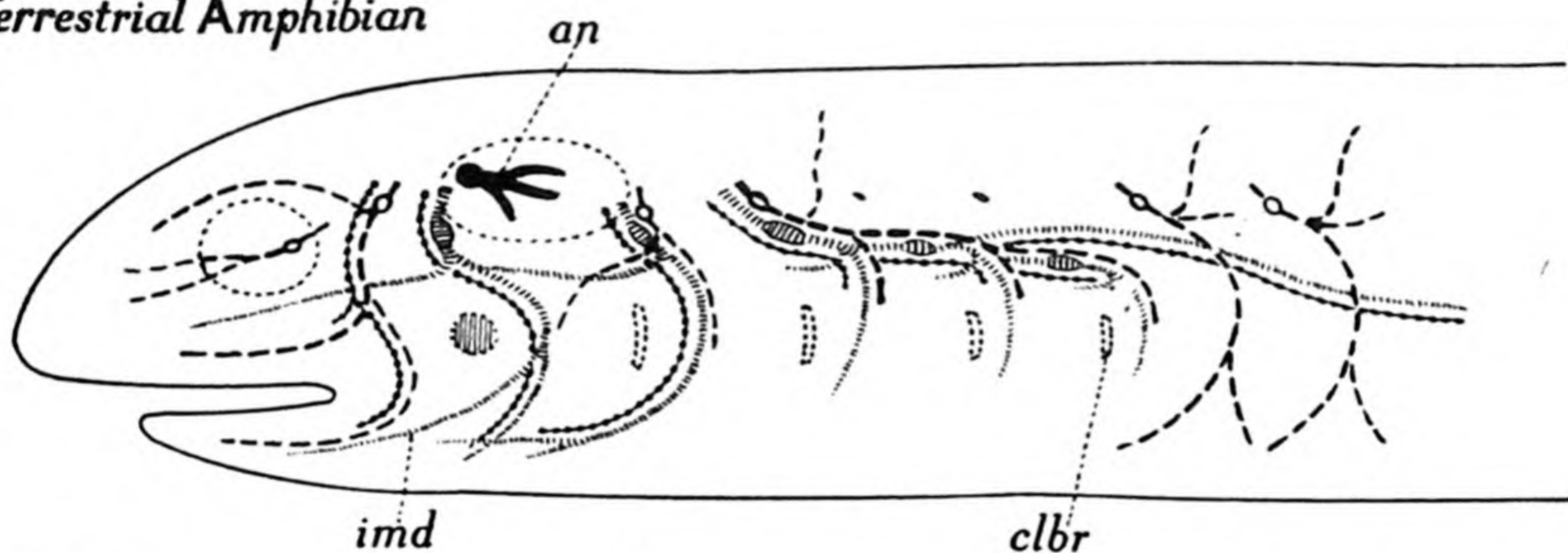
Amniote
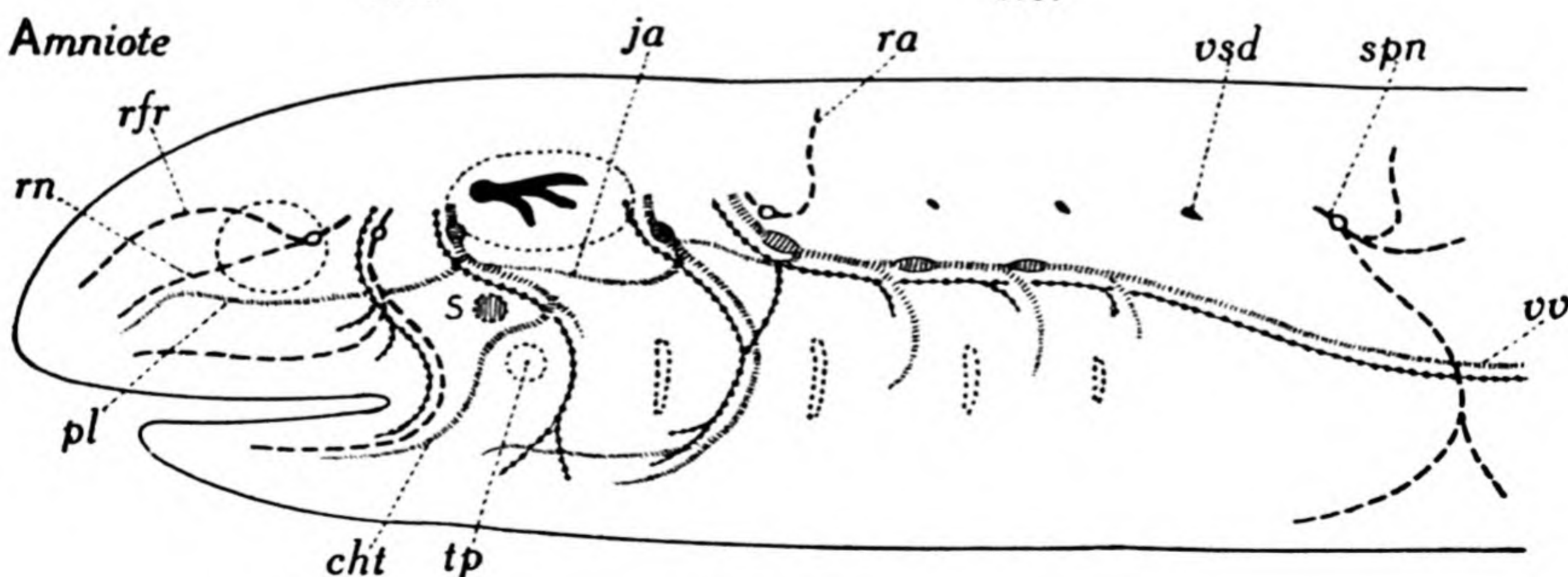
FIG. 728.

ost, sup. ophthalmic of trigeminal; pf, profundus; ph, pharyngeal; pl, palatine; pr, pretrematic; pt, postrematic; ra, dorsal ramus; rac, recurrent accessory ramus of facial and of vagus; rbf, buccal; rfr, ramus frontalis; rhm, hyomandibular; rn, orbitonasal; ro, ramus oticus; rst, r. supratemporalis; s, spiracular slit; spn, dorsal root of spinal nerve; tg, trigeminal; tp, tympanic membrane; vsd, vestigial dorsal root; vg, vagus; vv, visceral ramus. Components: black line = lateral line; broken line = general cutaneous; beaded line = visceral motor; cross-hatched line = visceral sensory.

the sensory branch of the segment behind. These dorsal rami supply the skin of the dorsal region and the muscles of the median fin (p. 116). A

mixed ramus medialis innervates the dorsal part of the myomere above the horizontal septum and the skin of that region, and a mixed ramus ventralis innervates the ventral part of the myomere and the skin of the latero-ventral region. Visceral motor and sensory fibres pass to the ' sympathetic ' by the ramus communicans (p. 775).

The Cranial Nerves :—We may now briefly review the nerves of the head in order from before backwards, Fig. 728. The first is the nervus terminalis composed of general cutaneous fibres.

The **nervus terminalis,** first clearly described by Pinkus in *Protopterus* (1161), has since been found in all Gnathostomes from sharks to man (Locy, 1145, in Selachii ; Brookover, 1910, Sheldon, 1909, in Teleostomi ; Pinkus, 1894, Bing and Burkhardt, 1905, in Dipnoi ; Herrick, 1909, McKibben, 1911, in Amphibia ; Johnston, 1913, Larsell, 1919, in Reptilia ; Brookover, 1914, 1917, Johnston, 1914, Huber and Guild, 1913, Larsell, 1918, Stewart, 1175, in Mammalia). This nerve, not to be confused with the vomero-nasal division of the olfactory nerve with which it is often closely associated for part of its course, issues from the fore-brain (telencephalon) near the recessus neuroporicus and lamina terminalis, has a ganglion (ganglion terminale) and peripheral fibres distributed to free nerve-endings chiefly in the region of the nasal septum and external nostril. Van Wijhe, 1918, considers the n. terminalis to be the homologue of the first or apical nerve of *Amphioxus*, also a sensory nerve with ganglion cells on its course and distributed to the rostrum (Ayers, 1919).

Profundus Nerve.—Well developed and distinct in Cyclostomes this nerve becomes closely related or even fused to the trigeminal in Gnathostomes, and for a long time was considered to be a part of it,[1] until Marshall (366), van Wijhe (396), and others showed that it is the dorsal nerve of the premandibular segment with its own ganglion. The general cutaneous fibres of which it is almost entirely composed innervate the skin of the anterior region of the head, especially the snout and neighbourhood of the nostril. It is variable in size in Pisces, consisting typically of two chief branches : a main longitudinal ramus ophthalmicus profundus (r. nasalis, or nasociliaris) which crosses the orbit between the dorsal and ventral divisions of the oculomotor, dorsally to the optic nerve, and between the superior and inferior oblique muscles of the eye, passing through the nasal capsule to the snout (Chapter VI.) ; and a more dorsal ramus frontalis or portio ophthalmicus profundi, which in Pisces usually joins the superior ophthalmic branches of the facial and trigeminal nerves. The

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[1] Consequently the profundus is often called V¹, the r. maxillaris V², and the r. mandibularis V³.

r. frontalis may be much reduced in some Selachians and Teleostomes (being then apparently replaced by the r. ophth. superf. trigemini), or well developed and separate as in *Polypterus* (Allis, 410). The r. ophth. profundus may also disappear in Selachians (*Scyllium*) and Teleosts, leaving only the radix longa to the ciliary ganglion and long ciliary nerves which always arise from it (p. 774). The r. frontalis remains an important branch in Amniota, as well as the r. nasalis.

The second nerve of *Amphioxus*, a sensory root-nerve with ganglion cells on its course, is considered by van Wijhe to be the homologue of the profundus nerve of Craniates (1918).

Trigeminal Nerve.—From the trigeminal or Gasserian ganglion come two main branches : a general cutaneous ramus maxillaris to the region of the upper jaw, and a mixed visceral motor and general cutaneous r. mandibularis. The former becomes closely connected with the buccal branch of the facial. The r. mandibularis supplies sensory fibres to the region of the lower jaw, and motor fibres to constrictor muscles and their derivatives (constrictor superficialis dorsalis of this segment, adductor mandibulae, levator labialis superioris, levator maxillae sup. of Pisces, also protractor hyomandibularis, dilator operculi, levator arcus palatini of Teleostomi ; masseter or temporalis or capiti-mandibularis, pterygoideus anterior and posterior of Amphibia, Reptilia, and Aves ; masseter, temporalis pterygoideus internus and externus, digastricus (pars anterior), tensor veli palatini, and tensor tympani of Mammalia).

The ramus ophthalmicus superficialis forms a general cutaneous third branch more dorsal and so closely associated with the r. frontalis profundi and r. ophth. superf. facialis that it is doubtful how far these sensory fibres really belong to the trigeminal. In Amniota it is no longer distinguishable from the r. frontalis.

Facial Nerve.—The facialis bears the Geniculate ganglion and contains all the dorsal components in Teleostomes, but loses the general cutaneous almost if not entirely in Elasmobranchs, Amphibia, and Amniota. The latter, of course, have no lateralis component left in the facial nerve. Lateralis fibres pass ventrally into the postspiracular truncus hyomandibularis, and are distributed more dorsally in rami oticus, ophthalmicus superficialis, and buccalis (certain neuromasts on the trunk are supplied by a recurrent r. lateralis in Amphibia) ; these lateral-line branches disappear in terrestrial forms. In Teleosts visceral sensory fibres pass into rr. maxillaris and mandibularis trigemini to supply the inner surface of the jaws and teeth, and in those forms with external taste-buds visceral fibres run to them in these nerves and the r. ophth. superficialis. The external taste-buds farther back are supplied by a special dorsal recurrent

branch of the facialis, with which a similar branch from the vagus combines to form the ramus 'lateralis accessorius'; lateralis fibres may enter this nerve, and the spinal nerves may contribute general cutaneous fibres to it. The well-developed pharyngeal branch of visceral sensory fibres in all Gnathostomes runs forwards as the palatine (great superficial petrosal) nerve to the roof of the buccal cavity. A ventral branch from it supplies the roof of the buccal cavity posteriorly and in Pisces the anterior wall of the spiracle and spiracular pseudobranch; it represents the pre-trematic branch of the facialis nerve.

In most Osteichthyes and Tetrapoda (but not in Elasmobranchii) the pharyngeal branch of the glossopharyngeal joins the r. palatini facialis forming 'Jacobson's anastomosis'.

The post-trematic branch or truncus hyomandibularis carries lateralis fibres to the preoperculo-mandibular, oral, and jugal canals in aquatic forms, and supplies general cutaneous fibres to the region of the hyoid and lower jaw in a ramus mandibularis externus in Osteichthyes; a branch composed of these fibres also innervates the operculum. But in Selachians the general cutaneous component is small as in Notidani (Kappers, 1132), or said to be altogether absent as in *Squalus* (Norris and Hughes, 1158). Visceral sensory fibres form a r. mandibularis internus to the mucous surface of lower jaw and buccal cavity, including taste-buds (chorda tympani).

The distribution of these components of the tr. hyomandibularis in Amphibia closely resembles that of fishes; in Urodela it may divide into a lateralis r. mentalis, a visceral r. mandibularis internus (r. alveolaris), and a motor r. jugularis receiving general cutaneous fibres from the glosso-pharyngeal. In Amniota the r. mandibularis internus (combined with 'sympathetic' fibres) is known as the 'chorda tympani' (p. 462).

The motor fibres supply the constrictor muscles and their derivatives (adductor hyomandibularis, adductor and levator operculi of Osteichthyes; depressor mandibulae, part of mylohyoideus, sphincter colli and stapedial of Reptilia and Aves; pars posterior of digastric occipito-frontalis, stylo-hyoideus, stapedial, platysma, and facial muscles of Mammalia).

The auditory nerve with its ganglion is a special development of the acustico-lateral component of the facial segment with various branches supplying the sensory epithelium of the labyrinth. Though the rootlets of the auditory and facial nerves are separated in higher Gnathostomes, they are closely connected in Amphibia and Pisces, especially in early stages of ontogeny.

Glossopharyngeal Nerve.—This closely approaches in Pisces the ideal 'branchial nerve' described above, and contains usually all the dorsal

components excepting the general cutaneous.   Fibres of this component
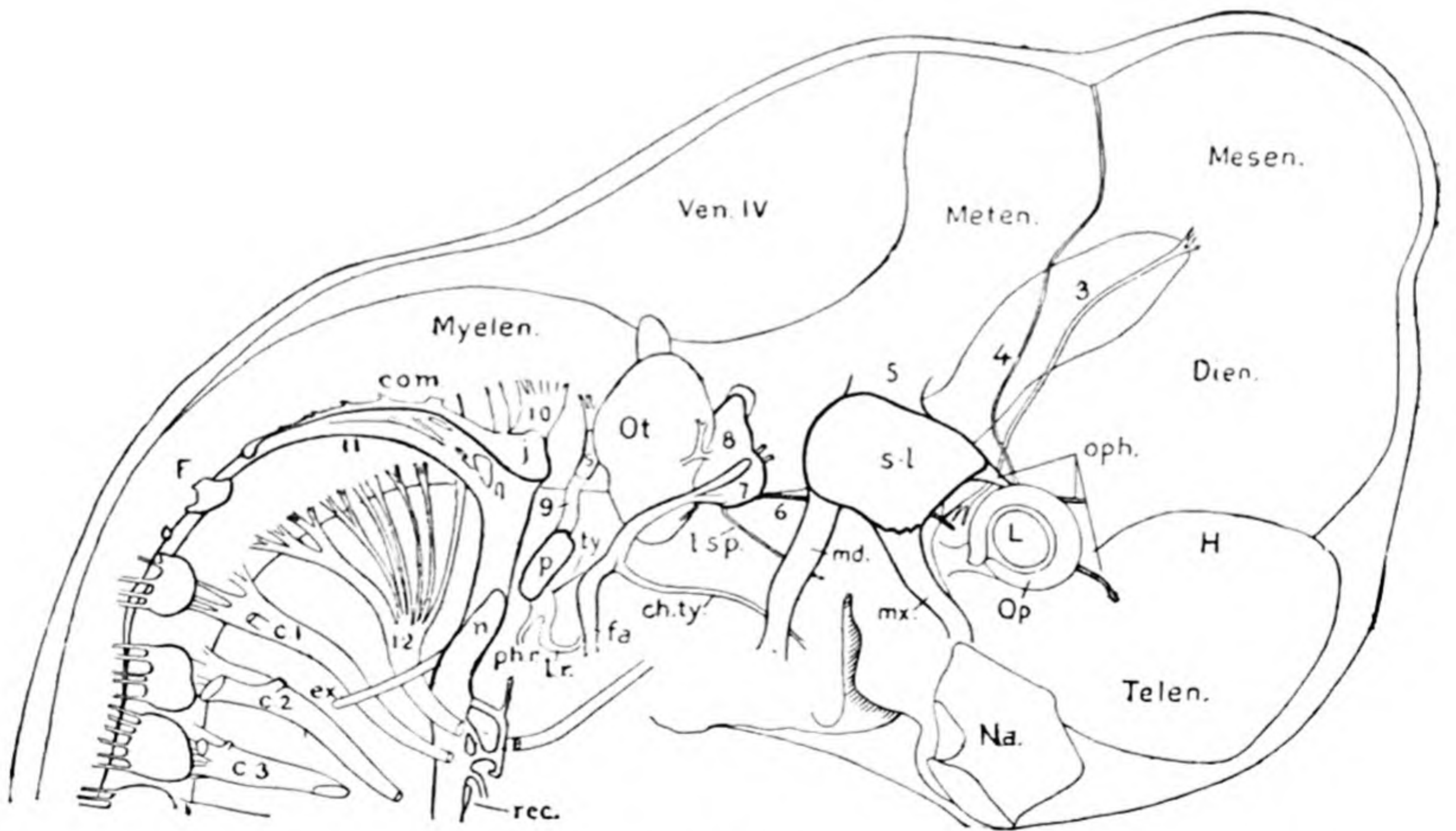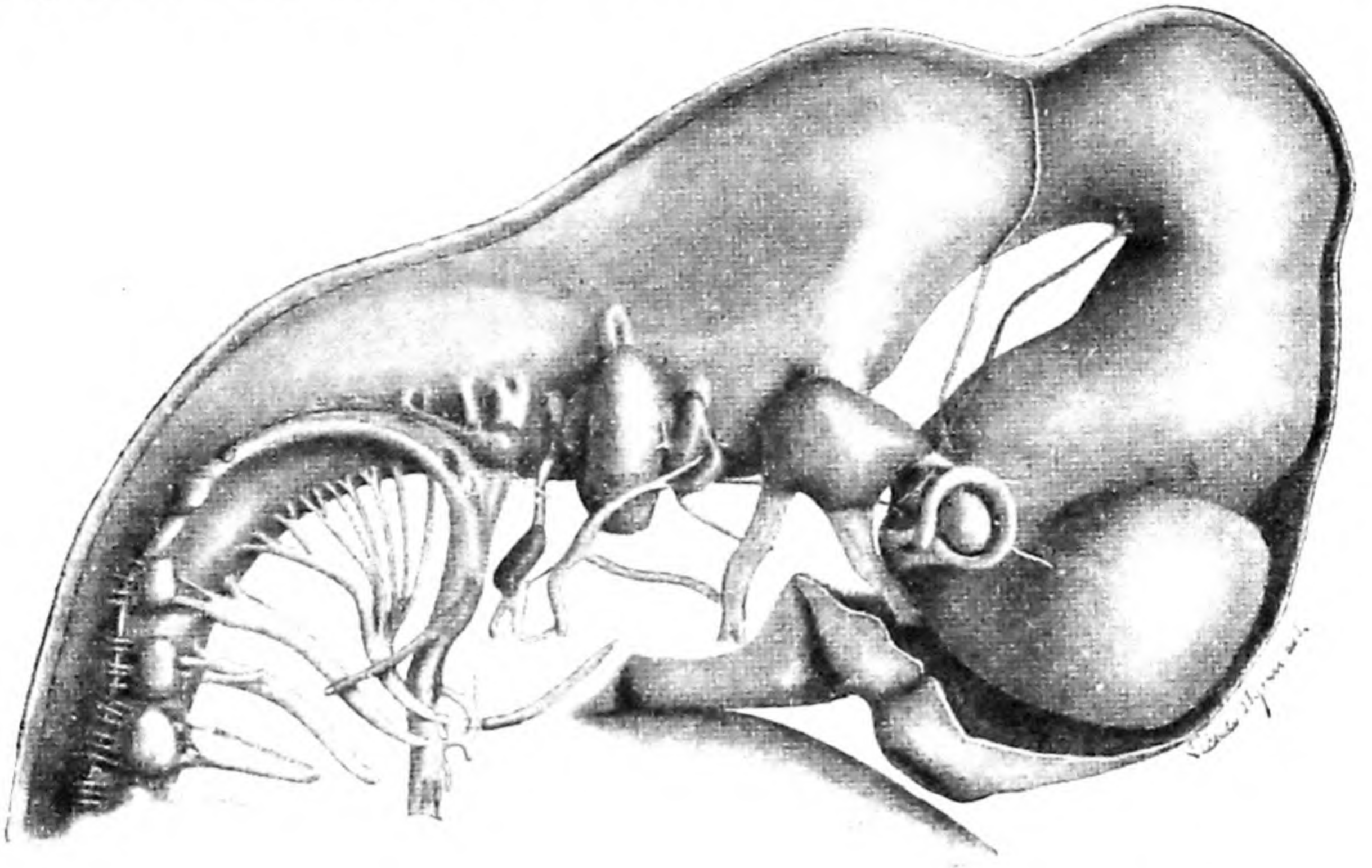
FIG. 729.

Reconstruction of brain and cerebral nerves of a 12 mm. pig embryo (from J. B. Johnston, *Nerv. Syst. of Vert.*, 1908, after Minot and Lewis). 3-12, Cranial nerves ; *s.l*, semilunar ganglion of trigeminal ; *oph*, profundus branches ; *l.s.p*, large superficial petrosal ; *ch.ty*, chorda tympani ; *fa*, main (hyomandibular) facial ; *s*, superior, and *p*, petrosal ganglion ; *ty*, tympanic ; *lr*, lingual, and *phr*, pharyngeal branches of glossopharyngeal ; *j*, jugular, and *n*, nodosal ganglion ; *rec*, recurrent n ; *ex*, spinal accessory branch to trapezius ; *F*, Froriep's vestigial ganglia ; $c^{1\text{-}3}$, cervical spinal nerves ; 12, hypoglossal.

are still present in some Elasmobranchs (Notidani, Kappers, **1132** ; *Mus-*

telus, Hauser ; *Laemargus*, Ewart and Cole, **1108** ; *Chimaera*, Cole, **1099**); they issue by the ramus supratemporalis, chiefly formed of the lateralis fibres of this segment. General cutaneous fibres also occur in Amphibia, pass to the facial by Jacobson's anastomosis or other branches, and into the post-trematic branch ; the dorsal fibres probably enter the r. auricularis of the vagus. This component has disappeared in Amniota. Visceral sensory fibres make up the r. pharyngeus (r. communicans IX ad VII, Jacobson's anastomosis, tympanic branch) and pre-trematic branches, and enter the post-trematic branch to supply the posterior ventral region of the buccal cavity and tongue by the r. lingualis in higher forms.

The post-trematic branch contains visceral motor fibres to visceral muscles of the 1st branchial arch (levator arcus branchialis, ceratohyoideus,
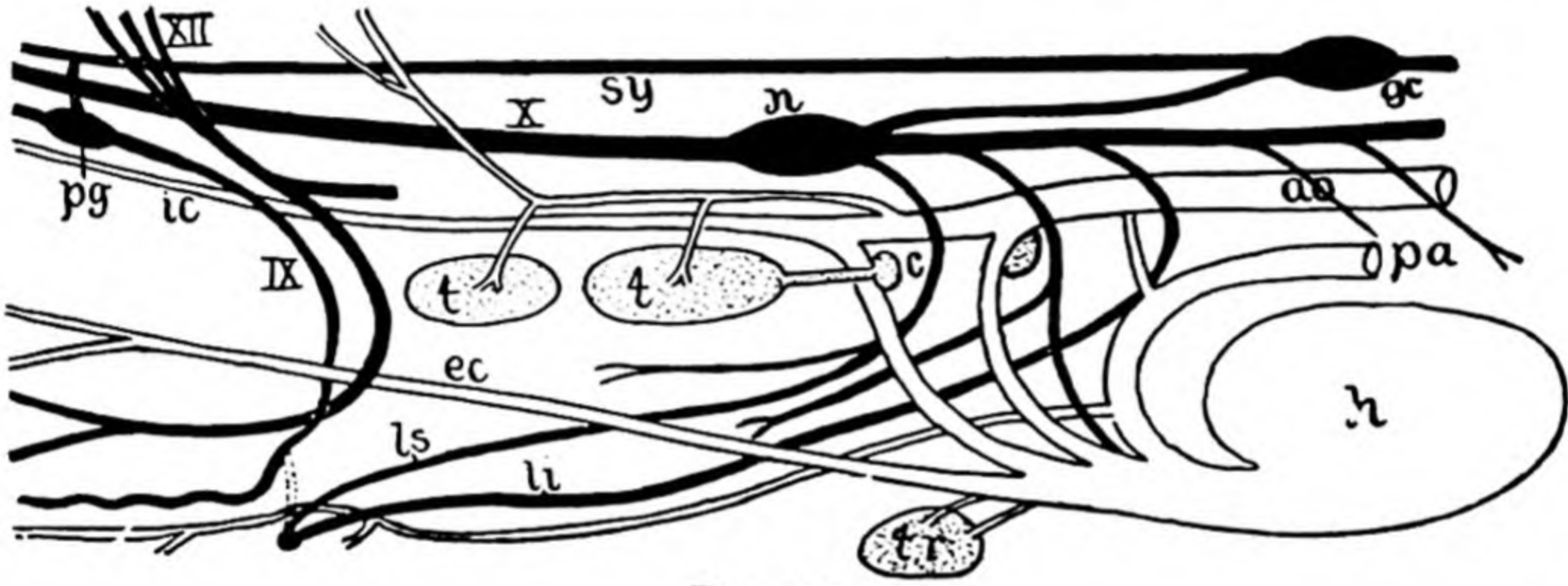
FIG. 730.

Diagrammatic left-side view showing relation of nerves and arteries in neck of *Sphenodon* (after van Bemmelen, from J. S. Kingsley, *Comp. Anat. of Vertebrates*, 1926). Nerves black, arteries white. *ao*, Dorsal aorta ; *c*, carotid gland ; *ec*, external carotid ; *gc*, cervical sympathetic ganglion ; *ic*, internal carotid ; *li, ls*, inferior and superior laryngeal nerves ; *n*, ganglion nodosum ; *pa*, pulmonary artery ; *pg*, petronal ganglion ; *sy*, sympathetic trunk ; *t*, thymus ; *tr*, thyroid.

and certain laryngeal muscles in Tetrapoda). The glossopharyngeal ganglion may be very closely connected with that of the vagus ; in Mammalia it becomes subdivided into a superior or jugular ganglion in the jugular foramen, and an inferior or petrous ganglion.

Vagus or Pneumogastric Nerve.—The largest of the cranial nerves is of compound origin (its general structure is discussed below, p. 767). Many rootlets lead to its ganglion jugulare or nodosum, Fig. 729. The lateralis fibres have already been dealt with (p. 742) ; they issue in a dorsal r. supratemporalis, a main r. lateralis, and smaller branches to the secondary dorsal and ventral lines of neuromasts.

Few general cutaneous fibres survive ; they pass dorsally in a r. auricularis, better developed in Teleostomes and Tetrapods than in Selachians. Visceral sensory fibres are distributed in Pisces, in pre- and post-trematic branches at each branchial slit, and to the dorsal wall of the pharynx by corresponding pharyngeal branches ; also by the large r. intestinalis to the

endodermal region of the alimentary canal and its glandular appendages and lungs, Fig. 730.

The visceral excito-motor fibres also pass to the alimentary canal by the r. intestinalis (p. 774), to visceral branchial muscles in Pisces, and corresponding muscles of hyoid apparatus and larynx in Tetrapoda. Some posterior motor rootlets of fibres supplying the trapezius muscle become separated off in Mammalia, and form a nerve called the eleventh cranial or spinal accessory nerve.

SPIRACULAR SENSE-ORGAN

The first or spiracular gill-slit is always specialised in Gnathostomes. Its opening is reduced in the course of ontogeny from below to a relatively
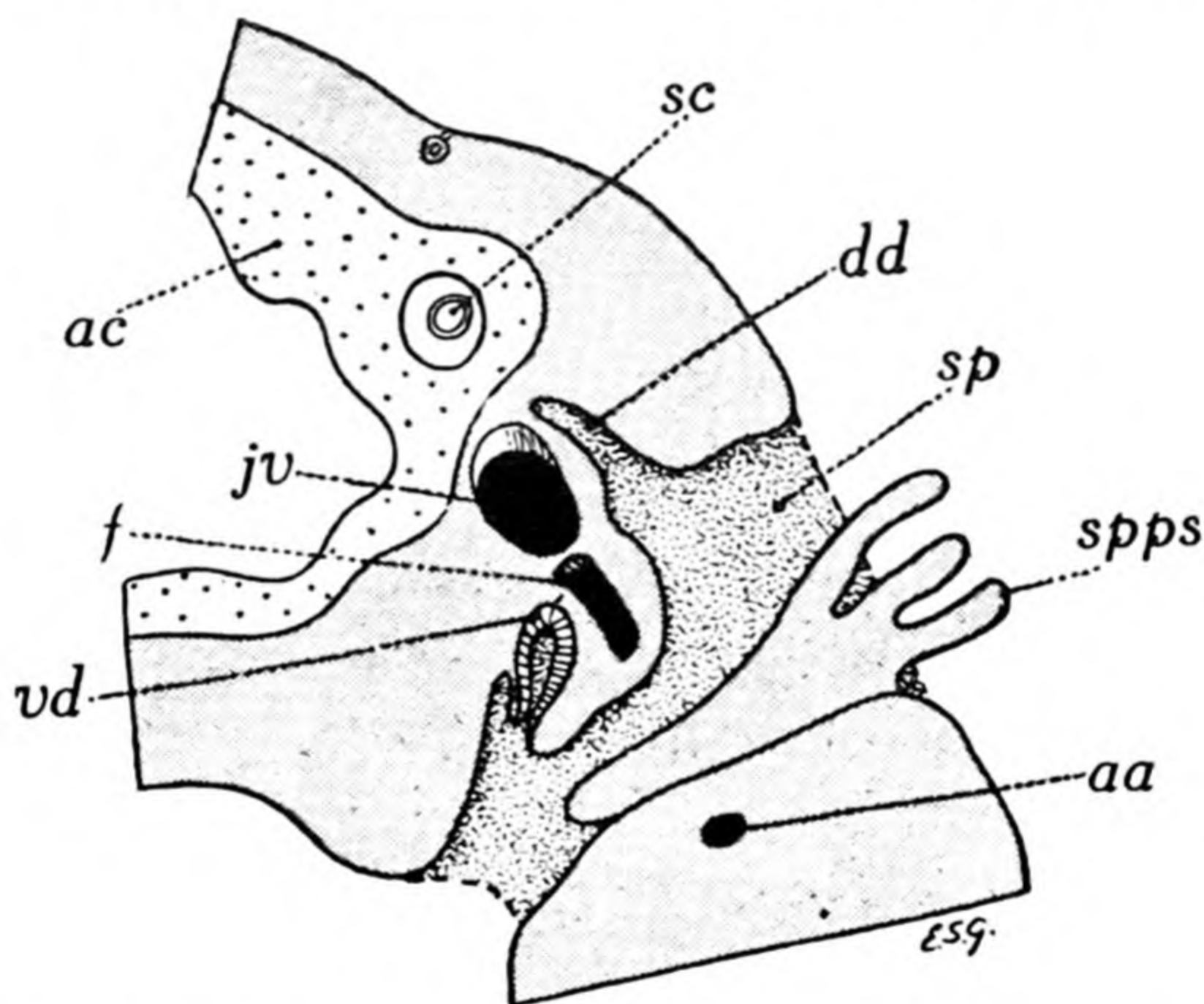
Fig. 731.

Scyllium canicula, advanced embryo. View from in front of transverse section through spiracle, diagrammatic reconstruction. *aa*, Afferent artery; *ac*, auditory capsule; *dd*, dorsal diverticulum; *f*, hyomandibular branch of facial nerve; *jv*, jugular vein (v. cap. lat.); *sc*, semicircular canal; *sp*, external opening of spiracular slit; *spps*, spiracular pseudobranch; *vd*, ventral diverticulum.

small spiracle situated behind the eye ; and even this aperture is closed in the adult of many Pisces (Holocephali, Dipnoi, most Teleostomi) and all Tetrapoda (p. 755).

It was long ago noticed by J. Müller (1841) that in many Selachians the spiracular slit gives off a dorsal diverticulum which becomes applied to the ventro-lateral wall of the auditory capsule below the prominence formed by the horizontal semi-circular canal, and morphologically ventrally to the articulation of the hyomandibula and jugular vein, Figs. 731-2. This ' auditory diverticulum ' possibly conveys vibrations to the

auditory labyrinth (J. Müller, 1833–43; v. Bemmelen, 1091; Ridewood, 1168).

Nearer the internal opening of the spiracular cleft there is another diverticulum from its anterior wall, as shown by Wright; the blind end of this diverticulum contains a neuromast sense organ (supplied by the otic branch of the facial) and in late stages becomes constricted off as a closed vesicle (Hoffmann, 354; van Wijhe, 1183; Norris and Hughes, 1158). A similar neuromast was discovered by Wright (1186) in *Acipenser*, *Lepidosteus*, and *Amia*, where it is lodged in a dorsal diverticulum of the spiracle, Fig. 733. This diverticulum passes up outside the wall of the
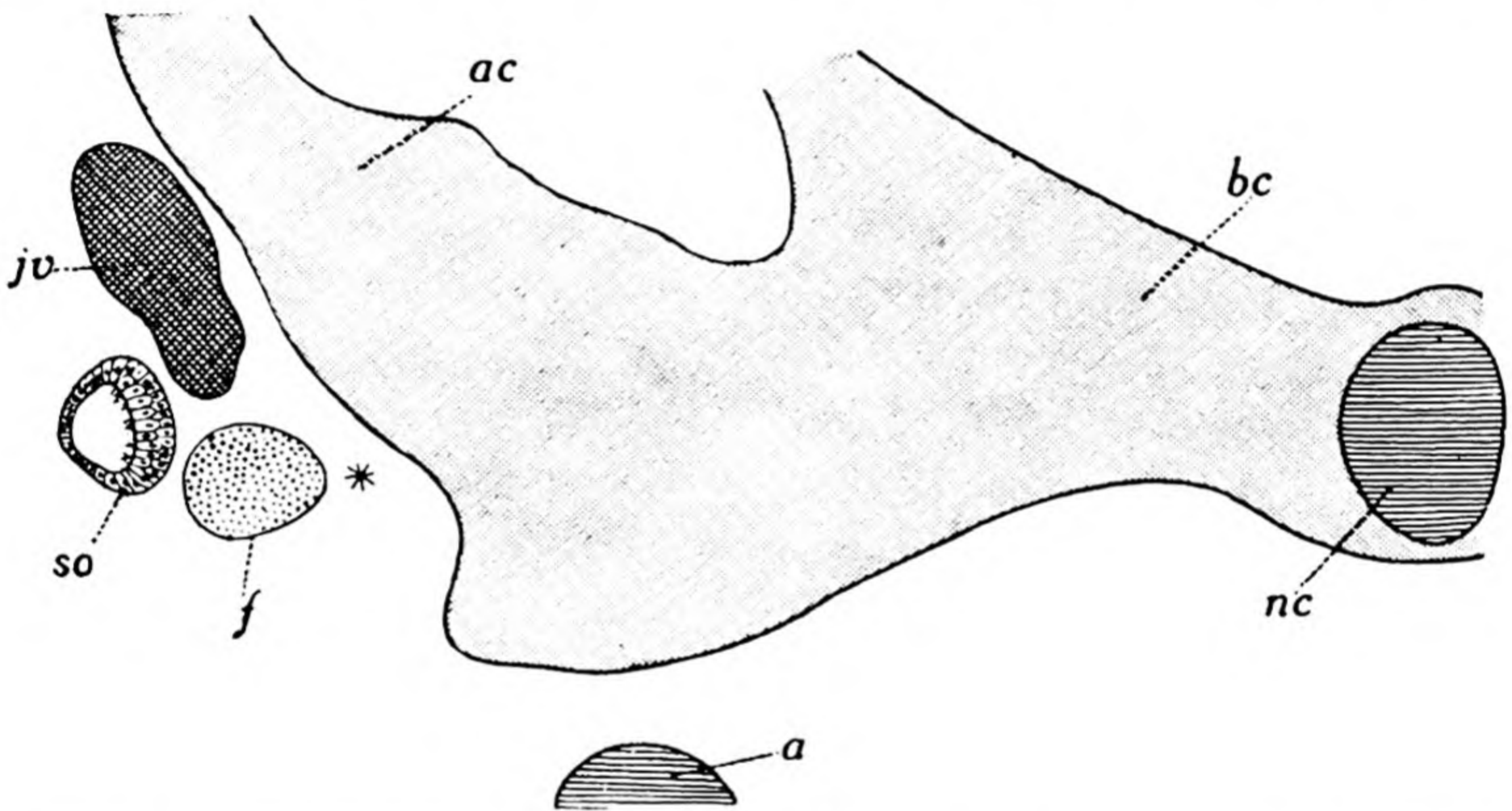
FIG. 732.

Portion of transverse section through auditory region of head of late embryo of *Heterodontus* (*Cestracion*) *Philippi*, 70 mm. long. *a*, Lateral aorta; *ac*, auditory capsule; *bc*, basal plate; *f*, hyomandibular branch of facial nerve; *jv*, jugular vein (v. capitis lateralis); *nc*, notochord; *so*, spiracular sense organ in vesicle closed off from diverticulum of spiracular slit, a star marks position of more posterior and ventral diverticulum (cp. Fig. 731).

trigemino-facialis chamber in front of the hyomandibula, its blind end projecting dorsally through a canal piercing the postorbital process, and the neuromast being there supplied by a twig of the otic branch of the facial nerve. The canal is formed by overgrowth of cartilage from the capsule in front and wall of the trigemino-facialis chamber behind. The Dipnoi also possess a spiracular sense-organ discovered by Pinkus (1611) in *Protopterus*, where it is in the form of a closed vesicle lodged in the cartilaginous postorbital process. Agar (1079) has shown that in *Lepidosiren* it arises as an offshoot from the ectodermal region of the spiracle. There can be no doubt that the spiracular sense organ of all these fishes is a special neuromast, derived from that part of the acustico-lateral system supplied by the otic nerve, which has sunk into the spiracle. The interesting sense-

organ recently described by Vitalli (1179-80) in a vesicle between the tympanic cavity and the auditory capsule in Birds is possibly of the same nature (Ranzi, 1165).
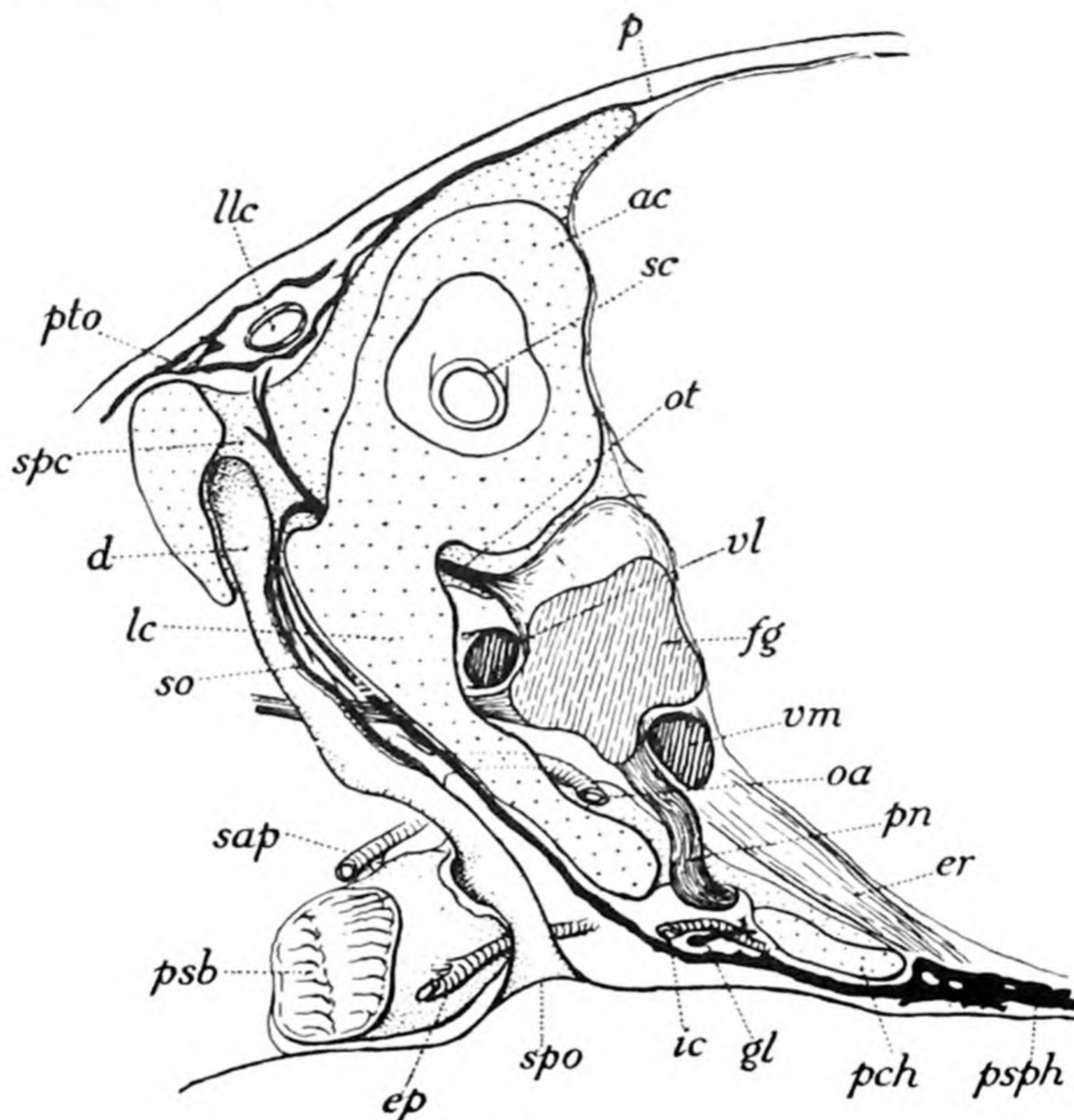
FIG. 733.

Reconstructed thick transverse section of head of larval *Amia* showing spiracular sense-organ in dorsal diverticulum of spiracular pouch. *ac*, Auditory capsule; *d*, dorsal diverticulum of spiracular pouch penetrating into spiracular canal; *ep*, efferent pseudobranchial artery; *er*, posterior or external rectus; *fg*, portion of facial ganglion in trigemino-facial chamber; *gl*, visceral branch of glosso-pharyngeal; *ic*, internal carotid in parabasal canal; *lc*, lateral cartil. commissure, outer wall of trigemino-facialis chamber; *llc*, postorbital lateral-line canal; *oa*, orbital artery; *ot*, otic branch of facial supplying spiracular neuromast and lateral-line; *pch*, anterior parachordal cartilage; *pn*, palatine nerve passing forwards; *psb*, spiracular pseudobranch; *psph*, parasphenoid with lateral ascending wing; *sap*, secondary afferent pseudobranchial artery; *sc*, semicircular canal; *so*, spiracular neuromast; *spc*, spiracular canal in cartilage; *spo*, opening of spiracular pouch; *vl*, vena lateralis; *vm*, vena medialis. Posterior view.

THE DEVELOPMENT OF THE PERIPHERAL NERVOUS SYSTEM

Considerable light is thrown on the structure of the peripheral nervous system by a study of its development, of which only a brief sketch can here be given.

The central nervous system (brain and spinal cord) is developed in all Vertebrates from a single essentially unsegmented dorsal neural plate of thickened ectoderm which sinks inwards and folds to form a hollow tube. The two edges of the plate or neural folds coming together dorsally and

fusing become separated off from the superficial general ectoderm. The tube closes first in the anterior trunk region and then progressively from that point backwards and forwards. At the hind end the blastopore becomes enclosed by the neural folds and persists as a rule for a time as a neurenteric canal leading from the neural canal above to the cavity of the enteron below. Growth in length of all the germ-layers takes place here, more especially at the dorsal lip of the blastopore. The last point to remain open anteriorly is the temporary neuropore, which finally closes in
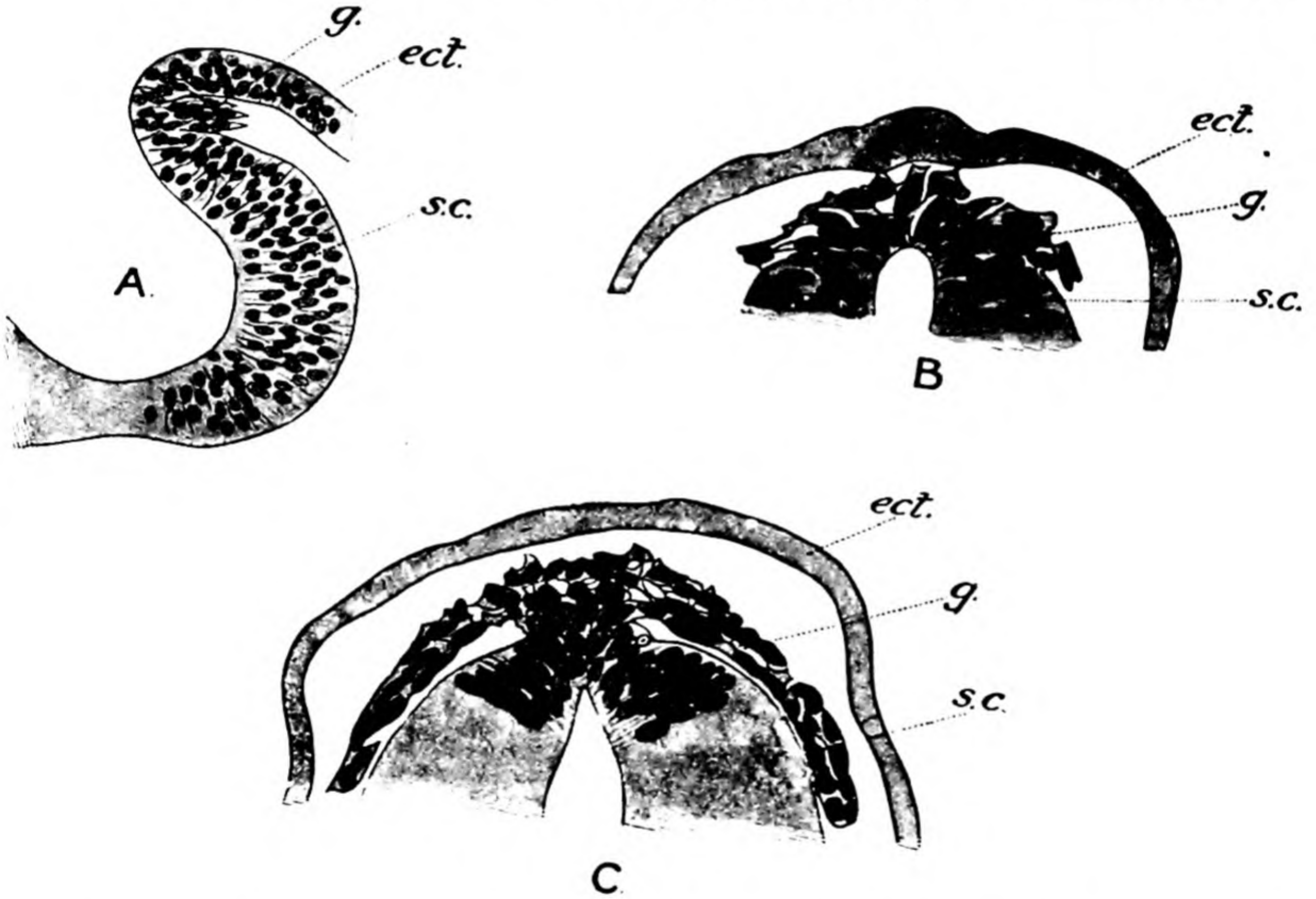
FIG. 734.

Transverse sections illustrating the mode of origin of the spinal ganglia. A, Fowl embryo with four mesoderm segments (after Neumayr, 1906); B and C, *Torpedo* 4 mm. embryo (after Dohrn, 1902). *ect*, Ectoderm; *g*, rudiment of ganglion; *s.c*, spinal cord. (From Kerr, *Embryology*, 1919).

front of the neural plate, and may be marked in later stages by a small depression on the inner face of the lamina terminalis of the brain, the recessus neuroporicus. The whole central nervous system thus soon forms a closed tube entirely surrounded by mesoblastic tissue; but while the neural plate is separating from the external ectoderm there appears along each side a longitudinal ridge or thickening of ectodermal cells, the neural crest of Marshall (366) and Beard (1089), Figs. 734-5. The exact time at which the crest appears varies in different regions and in different animals; it may appear when the neural folds meet, or a considerable time before as in the cerebral region of most forms. When the separation of the external ectoderm from the neural tube has taken place

the crests remain attached to the latter and may meet in the middle line temporarily. The crests may be considered as proliferations of a narrow zone differentiated in the ectoderm along the edges of the neural plate, or perhaps as a differentiation of the margin of the plate itself. Probably the crest is primitively continuous from neuropore to blastopore. Segmental proliferations of the cells of the neural crest soon appear in the spinal region and develop from behind the head to near the tip of the tail; as these segmental rudiments of the spinal ganglia enlarge and grow downwards between the neural tube and the outer mesoblastic somites the neural crest between them disappears. In the head region the neural
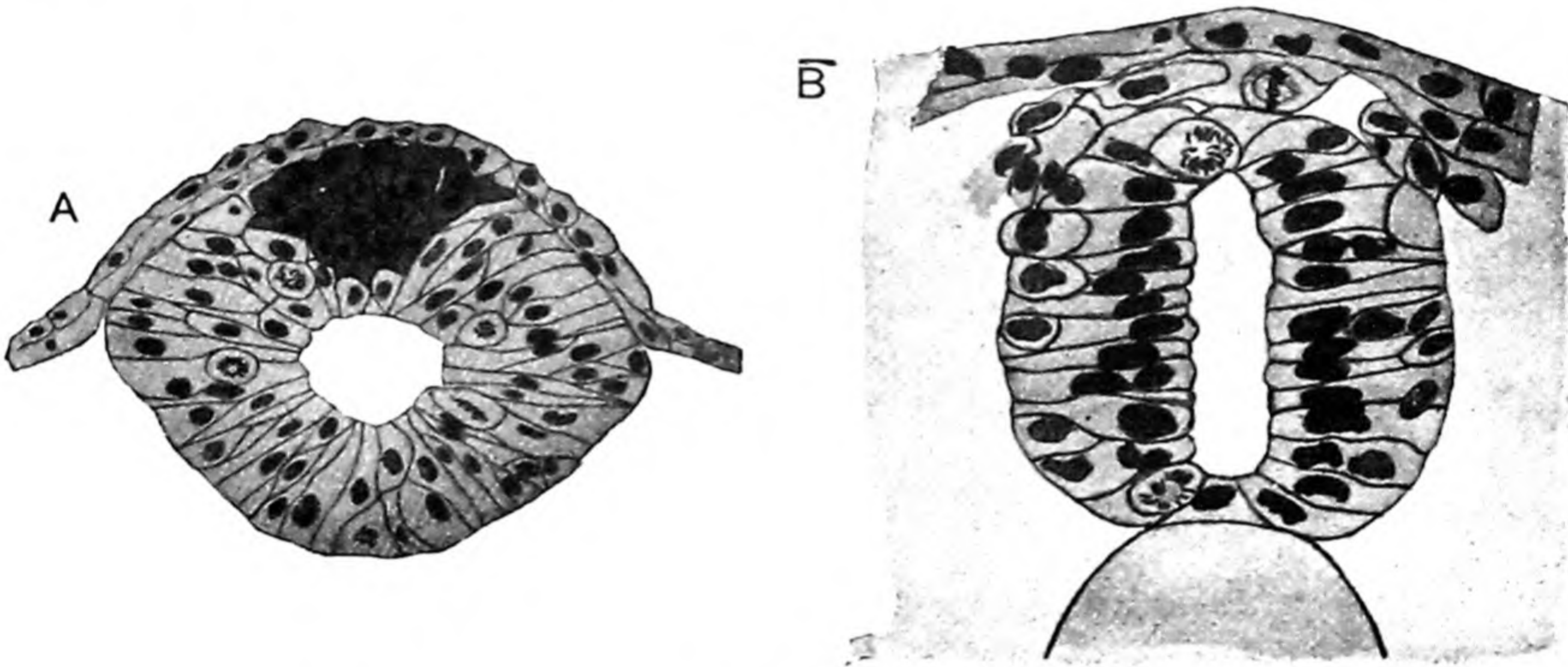
FIG. 735.

Transverse section of neural tube of embryo *Siredon* (*Amblystoma*) *punctatum*. Neural crest cells darkly shaded (from J. B. Johnston, *Nerv. Syst. of Vert.*, 1908). A, Just after closing; B, later stage.

crest becomes very early interrupted, and proliferations from it give rise to the rudiments of the vagus, glossopharyngeal, facial and auditory, trigeminal and profundus ganglia, Figs. 736-9 (Balfour, 317; Marshall, 366; van Wijhe, 396; Beard, 1089; His, 1879–93, and others; more recent general accounts will be found in text-books, more especially in those of Neumayer, 1164; Keibel and Mall, 1910–12; Brachet, 993; Johnston, 359). The nervus terminalis probably develops from its extreme anterior end.

The subsequent history of the development of the spinal nerves is comparatively simple. As the rudiments of the ganglia enlarge and grow downwards they lose their primitive connexion with the neural tube. Some of the indifferent crest-cells become ganglion cells or neurons, others become neuroglia and sheath-cells. The ganglion cells send a fibre growing inwards centripetally into the central nerve tube to form the definitive

dorsal afferent root, and a fibre growing outwards centrifugally to form the afferent nerve. The ventral root is formed by the outgrowth from cells in the neural tube of efferent fibres which pass outwards to the corresponding myotome. At first in Selachians (Balfour) this ventral root is separate, but it soon meets the dorsal root beyond the ganglion to form a mixed nerve which runs in the septum posterior to its myotome (the
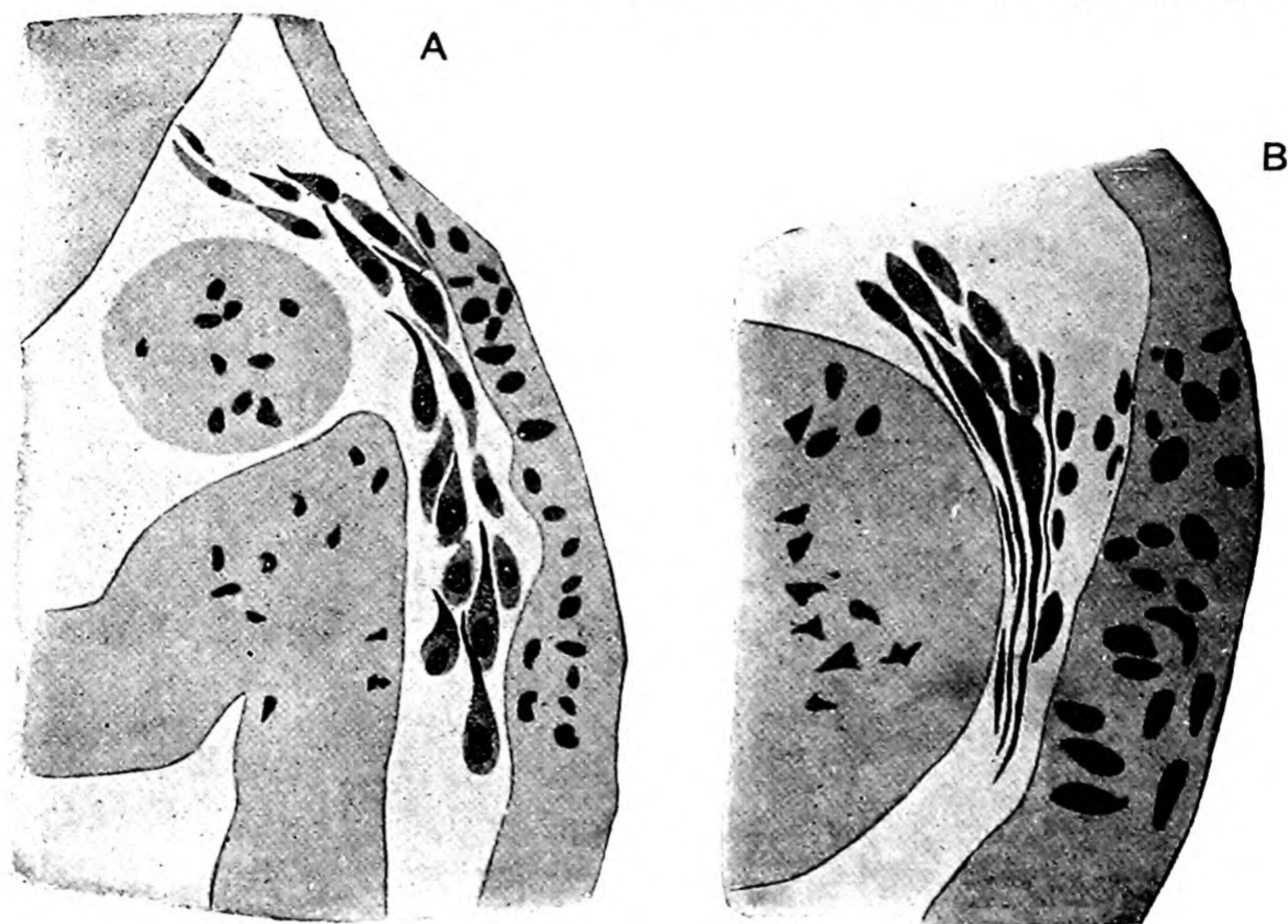
FIG. 736.

Transverse sections of embryo *Siredon* (*Amblystoma*) *punctatum* (from J. B. Johnston, *Nerv. Syst. of Vert.*, 1908). A, ganglion of glossopharyngeal at time of formation of central processes ; B, ganglion of trigeminal with outgrowing axons of ramus mandibularis.

segmental relationships of nerves and myotomes are discussed below ;

Particular interest attaches to the development of the cranial nerves and ganglia (Marshall, 366 ; v. Wijhe, 396 ; Beard, 1088-9 ; Froriep, 498 ; v. Kupffer, 363 ; Neal, 368 ; Kolzoff, 361 ; Dohrn, 1105 ; Landacre, 1142a-43a ; Belogolowy, 1090 ; Brachet, 993 ; Chiarugi, 1097 ; Goronowitsch, 1115-16 ; Klinkhardt, 1134 ; Neumayer, 1154 ; Guthke, 1117 ; Knouff, 1135).

These cranial ganglia and nerves seem to arise from three separate sources : (1) the neural crest ; (2) dorso-lateral placodes ; (3) epibranchial placodes. The neural crest, the chief source of the ganglionic cells, develops much as in the trunk, becoming early broken up into sections

which give rise by proliferation to segmental downgrowths. These rudiments of the ganglia, however, remain near the surface on the outer
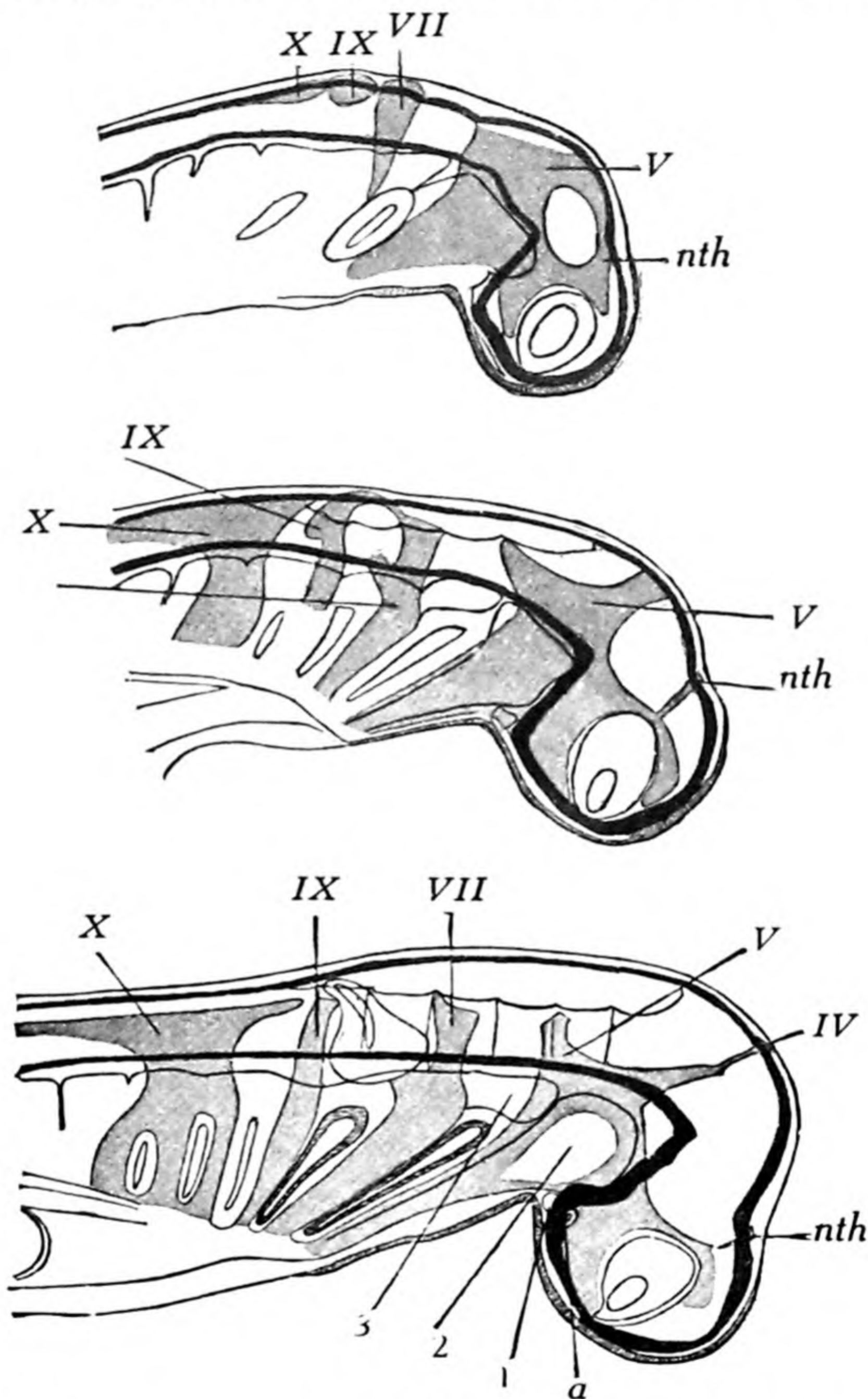
FIG. 737.

Diagrams of head-region of embryos of *Squalus acanthias* showing contribution from neural crest to development of cranial nerves (after H. V. Neal, from J. B. Johnston, *Nerv. Syst. of Vert.*, 1908). *a*, Anterior mesoblast (' head cavity ') ; 1, 2, 3, prootic somites ; cranial nerves *IV-X* ; *nth*, temporary nervous thalamicus.

side of the mesoblastic somites, here little developed. They develop at first intersegmentally (Neal, 368), that is posteriorly to the somite to which they are assigned (p. 219). The first proliferation gives rise to the profundus ganglion [1] (ganglion ophthalmicum, or mesocephalicum), which

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[1] Considerable confusion has arisen in the literature owing to this rudiment being named by several embryologists the ciliary ganglion (v. Wijhe, 396 ;

is usually closely associated with the next trigeminus or Gasserian ganglion. From the second rudiment, extending down into the hyoid arch, develops
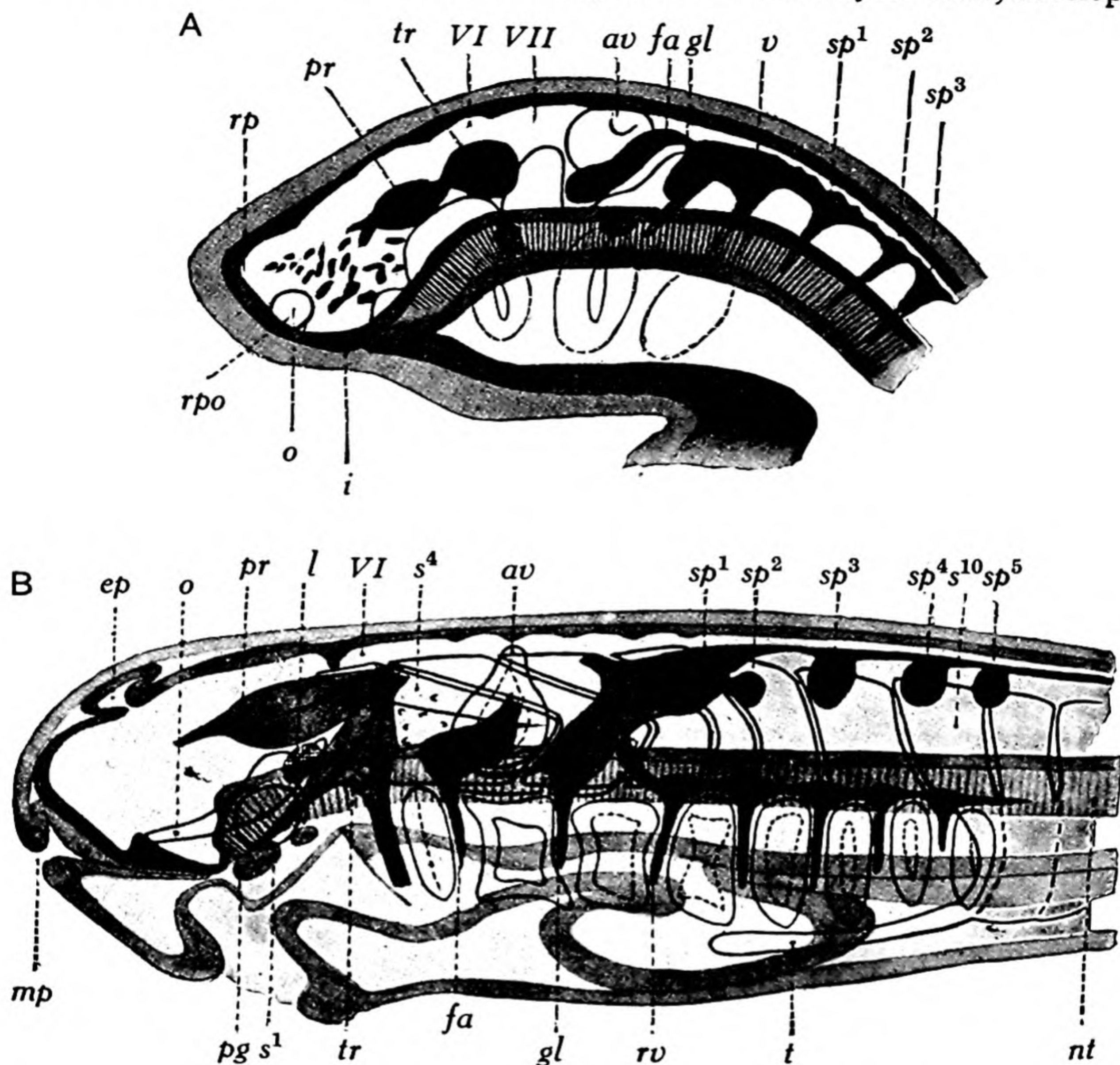
FIG. 738.

Reconstructions of head region of embryo *Petromyzon*, left-side view (after N. K. Koltzoff, from J. B. Johnston, *Nerv. Syst. of Vert.*, 1908). A, Young stage, with 2 gill-slits open and showing 3 prootic and 5 metaotic somites; B, older stage, 4 mm. long. *av*, Auditory vesicle; *ep*, epiphysis; *i*, infundibulum; *l*, lens; *mp*, median nasal pore; *nt*, notochord; *o*, optic cup; *pg*, preoral endoderm; *rp*, recessus neuroporicus; *rpo*, recessus preopticus; *rv*, post-trematic branch of vagus; s^1, premandibular somite, s^2, mandibular somite is just posterior to it; s^4, first metaotic somite; sp^{1-5}, dorsal root nerves of spinal region; *t*, hypoglossal muscle; *VI, VII*, neuromeres. Other letters as in Fig. 741.

the facialis or geniculate and the acusticus ganglia; and from the third, extending into the first branchial arch, arises the glossopharyngeus ganglion. A more extensive region of the neural crest gives rise to the compound vagus ganglion (composed of ganglia, each corresponding to

Klinkhardt, 1134, and others). The true ciliary ganglion belongs to the sympathetic system (p. 774).
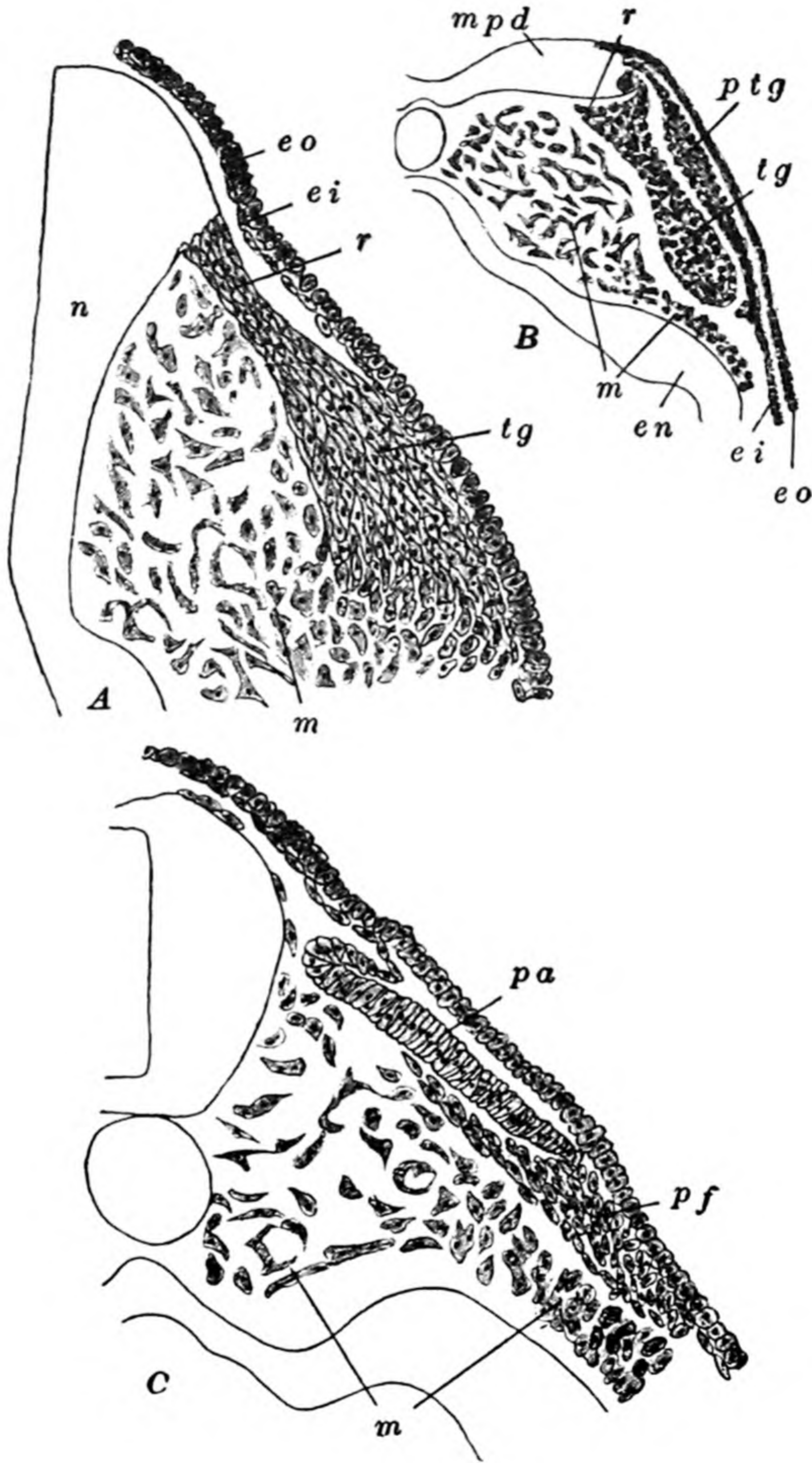
FIG. 739.

Portions of sections through head of frog (*Rana fusca*), illustrating formation of placodes and history of crest ganglia after Brachet, from W. E. Kellicott, *Chordate Develt.*, 1913). A, Transverse section through trigeminal ganglion of embryo, 3 mm. B, Transverse section through acustico-facialis ganglion of embryo with three or four pairs of mesodermal somites. C, Transverse section through facial ganglion and auditory placode of embryo, 2·8 mm. *ei,* Inner or nervous layer of ectoderm; *en,* endoderm; *eo,* outer layer of ectoderm; *m,* mesoderm; *mpd,* definite medullary plate; *n,* nerve cord; *pa,* auditory placode; *pf,* facial placode; *ptg,* trigeminal placode; *r,* spinal prolongation of ganglion; *tg,* trigeminal ganglion.

one branchial segment) and sends downgrowths into the remaining branchial arches, Figs. 736-9, 740.[1]

In the branchial region the rudiment of each cranial ganglion derived from the neural crest comes into contact with a thickening of the ectoderm at the dorsal edge of the corresponding gill-slit. These thickenings are the epibranchial placodes or 'branchial sense organs' of Beard (1088) and Froriep (1887). There is no sufficient evidence that they are or ever have been branchiomeric organs of sense, although it is possible that they give rise to cells from which develop the taste-buds. Each placode proliferates inwards producing a mass of cells which joins the neural crest rudiment, becomes detached from the surface, and, sinking inwards, contributes to the definitive ganglion of its segment. Such epibranchial placodes occur in the embryo of all Craniates from Cyclostomes to Man related to the ganglia of the facial, glossopharyngeal, and each of the vagal segments, Fig. 741.

FIG. 740.

Transverse section immediately behind the first visceral pouch of chick embryo of thirteen somites (after Goronowitsch, from F. R. Lillie, *Develt. Chick*, 1919). *Ad*, Aorta descendens ; *c*, rounded mesenchyme cells ; *f*, proliferation of ectoderm from placode ; *g*, place where cells derived from neural crest unite with mesenchyme cells of periaxial mass ; *ms*, mesoderm ; *p*, spindle-shaped peripheral mesenchyme cells.

[1] As the rudiments of the definitive nervous system of the head become differentiated portions of the neural crest not directly used up may become scattered and mixed indistinguishably with the true mesoblastic mesenchyme. There is reason to believe that such scattered ectoderm cells go to build up the peripheral nerves, probably in the form of sheath-cells. It has frequently been stated that they give rise to 'mesectoderm', contributing to the formation of the connective tissues or even the endo-skeleton of the head, with the help of other cells said to be proliferated from the inner surface of the covering ectoderm (Platt, 1162 ; v. Kupffer, 363 ; Dohrn, 1105, and others). This doctrine of the formation of special " mesectoderm " in the head is, however, almost certainly founded on misinterpretations and erroneous observations on unsuitable material (Brachet, 993 ; Adelmann, 1078).

Another contact of the neural crest ganglia takes place more dorsally with thickenings of the ectoderm known as dorso-lateral placodes. There is a series of such thickenings of which the auditory placode giving rise by invagination to the auditory sac (developing later into the membranous labyrinth and its sensory patches) is the largest and most constant. The dorso-lateral placodes are best developed in aquatic Craniates, but may appear also in Amniotes in a reduced condition. In spite of statements to the contrary there is good reason to believe that they are merely the rudiments of the lateral-line organs and their nerves, and it is doubtful whether even in fishes they make any important contribution to the definitive nervous system other than the neurons concerned with the lateral-line system. (See further development of lateral-line system, p. 744.)

There are thus two longitudinal rows of segmentally arranged placodes: a dorso-lateral series and a ventro-lateral or epibranchial series—the latter related to each gill-slit and branchial nerve; the former possibly represented in addition in the trigeminal and profundus segments, Figs. 728, 741.

It is tempting to associate each of these three possible sources of ganglionic cells with components (Strong, 1176), and it has been concluded that the neurons of the general cutaneous and general visceral components are derived from the neural crest cells, those of the special somatic (lateral-line system) component from the dorso-lateral placodes, and those of the special visceral (taste-bud system) from the epibranchial placodes (Landacre, 1142-43a). In the lower Craniates these three main elements of the ganglia may remain fairly distinct even in the adult and have each its own rootlet. The above conclusion is in accordance with the observation that the dorsolateral placodes (excepting the auditory) are reduced in terrestrial forms, and that the epibranchial placodes are preserved and correspond to those segmental nerves which supply taste-buds; but it is difficult to reconcile with the view of Herrick and Johnston that the two special systems have been phylogenetically differentiated from the general systems. Much further evidence concerning the precise derivation of the functional neurons making up the peripheral ganglia is required before safe conclusions can be reached.

Observations about the origin of the cranial ganglia are still very contradictory. It should be remembered that in at all events many of the lower forms the appearance of definite proliferations is preceded in early stages by a transient thickening of the epidermis of the head over extensive areas of which the placodes and rudiments of the lateral-line organs are local developments, and that these are not always clearly marked off from

each other.   Also in higher forms vestiges of the placodes and rudiments may apparently occur which contribute little or nothing to the definitive nervous system.

It seems fairly well established in the case of the vagus and glosso-pharyngeal ganglia that the neural crest supplies the general cutaneous and general visceral portions, and that the special visceral portions come from the epibranchial placodes and lateralis portions from the dorso-lateral placodes.   More difficult is the interpretation of the acustico-facialis complex.   Here the special visceral is doubtless derived from the first epibranchial placode; and the general visceral, and what general
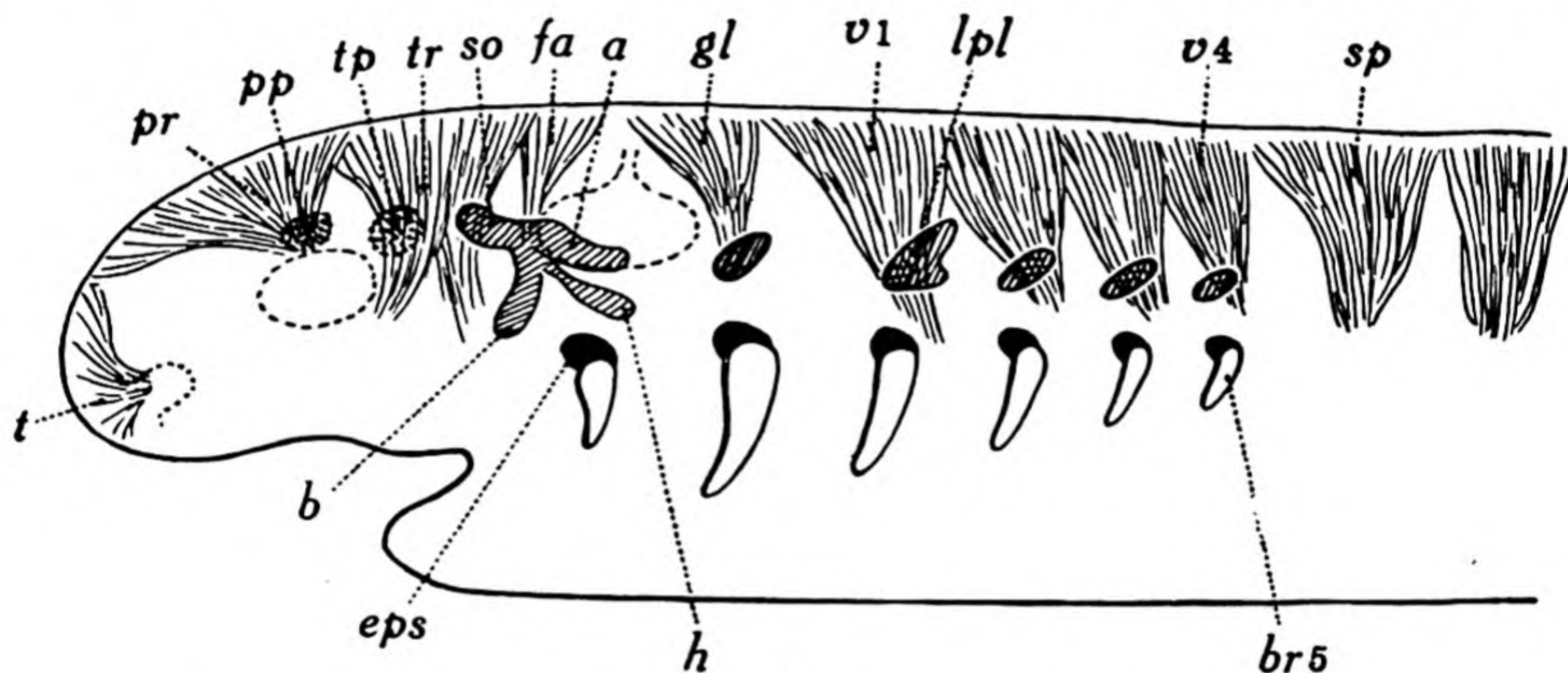
FIG. 741.

Diagram showing origin of segmental ganglia in Gnathostome.   Contribution from neural crest is striated, from dorso-lateral placodes obliquely hatched, from epibranchial placodes black.   a, Auditory branch ;   b, buccal branch ;   br5, fifth branchial gill-slit ;   eps, epibranchial placode of spiracular slit ; fa, facial ;   gl, glossopharyngeal ;   h, hyoid branch ;   lpl, lateral-line placode of vagus ;   pp, profundus placode ;   pr, profundus ;   so, superior ophthalmic branch ;   sp, spina ganglion ;   t, terminal ;   tp, placode of trigeminal ;   tr, trigeminal ;   v1-4, first to fourth segment of vagus.

cutaneous component there may be, from the neural crest.   There appear also in the lower forms a dorso-lateral and ventro-lateral placode in addition to the auditory placode, and all three should probably be con-sidered as differentiations from an extensive dorso-lateral placodal area from which are derived the auditory ganglion and the two lateralis portions of the facial ganglion.   But opinions differ as to the origin of the auditory ganglion in Amniotes, some deriving it more or less completely from the neural crest.   Concerning the origin of the trigeminal and profundus ganglia there is still less agreement.   Some would derive them entirely from neural crest cells (Goette, Corning, in Amphibia), others from both neural crest and dorso-lateral placodes or from the latter chiefly.   Most authors, however, describe a contact with the epidermis in the case of both these ganglia not only in the lower forms (*Petromyzon*: Kupffer, 363 ; Koltzoff, 361.   Selachians : Beard, 1089 ; Hoffmann, 354 ; Goette, 1114 ;

Klinkhardt, 1134; Gast, 1113; Guthke, 1117; de Beer, 1924. Amphibia: Brachet, 993; Knouff, 1135), but also in Birds (Goronowitsch, 1892-3; Neumayer, 1154) and Mammals (Chiarugi, 1097; Giglio-Tos, 1902: Adelmann, 1078).

Such a contact with the epidermis, even if temporary and not involving any contribution of cells, may indicate a vestigial lateralis ganglion belonging to the trigeminal segment. The profundus connexion is usually more pronounced and the ganglion seems to be derived, in considerable part at all events, from an epidermal placode. Now the profundus nerve is composed of general cutaneous fibres and has no lateralis component in Gnathostomes; we should expect it, therefore, to develop like a spinal ganglion from the neural crest. To explain this anomaly it has been suggested that the placode in this case belongs not to the dorso-lateral series but to the neural crest, which in the anterior region may spread outwards and so not become involved in the involution and sinking of the neural tube as it does farther back. The same explanation may apply to that part of the trigeminal ganglion which appears to develop from a dorso-lateral placode (Knouff, 1135).

Morphology of the Vagus.—There remains to be discussed the question of the morphology of the vagus nerve, which differs so markedly from the other nerves of the branchial region and supplies all the branchial arches behind the first. The known facts of its development and comparative anatomy do not allow us to explain this distribution of its branchial nerves as due to the branching of an originally single segmental nerve; nor do they support Gegenbaur's view that the vagus is a compound nerve formed by the gathering together of segmental dorsal nerves and ganglia equal in number to the gill-slits it supplies. This conception of the vagus as compounded of a number of complete dorsal nerves necessitates the further supposition that a corresponding number of myomeres have been compressed and more or less completely obliterated behind that corresponding to the first vagal segment, a supposition for which there is no evidence. If myomeres are suppressed at all it is immediately behind the auditory capsule (p. 226). Not only do the segments of the vagal region yield myomeres persistent in the adult, but there is developed in each of the vagal segments behind the first a pair of vestigial and usually transitory dorsal roots and ganglia, Figs. 240, 742. These were long ago described by Froriep in mammalian embryos (339), and are clearly seen in such lower forms as the Selachii (v. Wijhe, 396; Goodrich, 349; de Beer, 320). Whatever may be the explanation of the structure of the vagus, these vestigial segmental ganglia show that it has not been formed by their coalescence.

But the best evidence comes from a study of the anatomy and development of *Petromyzon* (Hatschek, 352 ; Koltzoff, 361; Johnston, 359, 1128). In this Cyclostome every segment in the region occupied by the vagus is provided with a myomere innervated by a ventral root nerve (coalesced in the first three metaotic segments), and a ganglionated dorsal root nerve giving off a dorsal general cutaneous ramus and a ventral branch connecting with the longitudinal ' epibranchial ' vagus. There has been
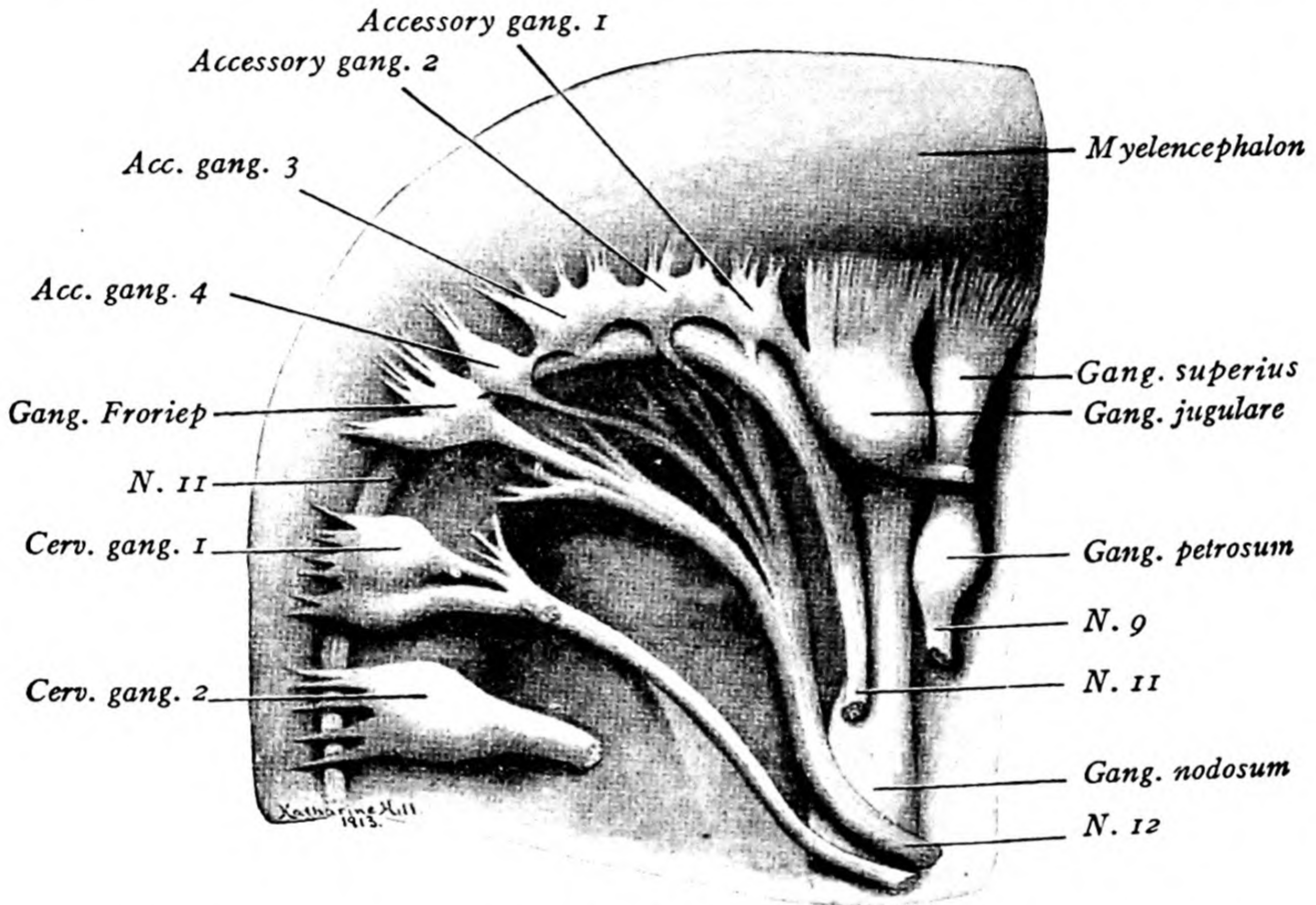
FIG. 742.

Dissection of head of 15 mm. pig embryo from right side to show accessory vagus ganglia with peripheral roots passing to hypoglossal nerve. × 25. (From Prentiss and Arey, *Textbook of Embryology*, 1917.)

here no general ' collecting ' of dorsal nerves and no suppression of segments, Figs. 728, 743.

Some other explanation must therefore be sought, and the best is based on the theory of partial polymerisation suggested in a general way by Hatschek. Adopting the doctrine of nerve components we may suppose that the rootlets of certain components of the segmental dorsal nerves supplying the branchial segments have been completely, as in the case of the special somatic and special and general visceral, or incompletely, as in the case of the general cutaneous components, gathered forwards into the anterior root of the vagus, some of the last component being left behind

in its original position (vestigial ganglia of Gnathostomes, and more complete dorsal nerves of Cyclostome). The longitudinal 'epibranchial'
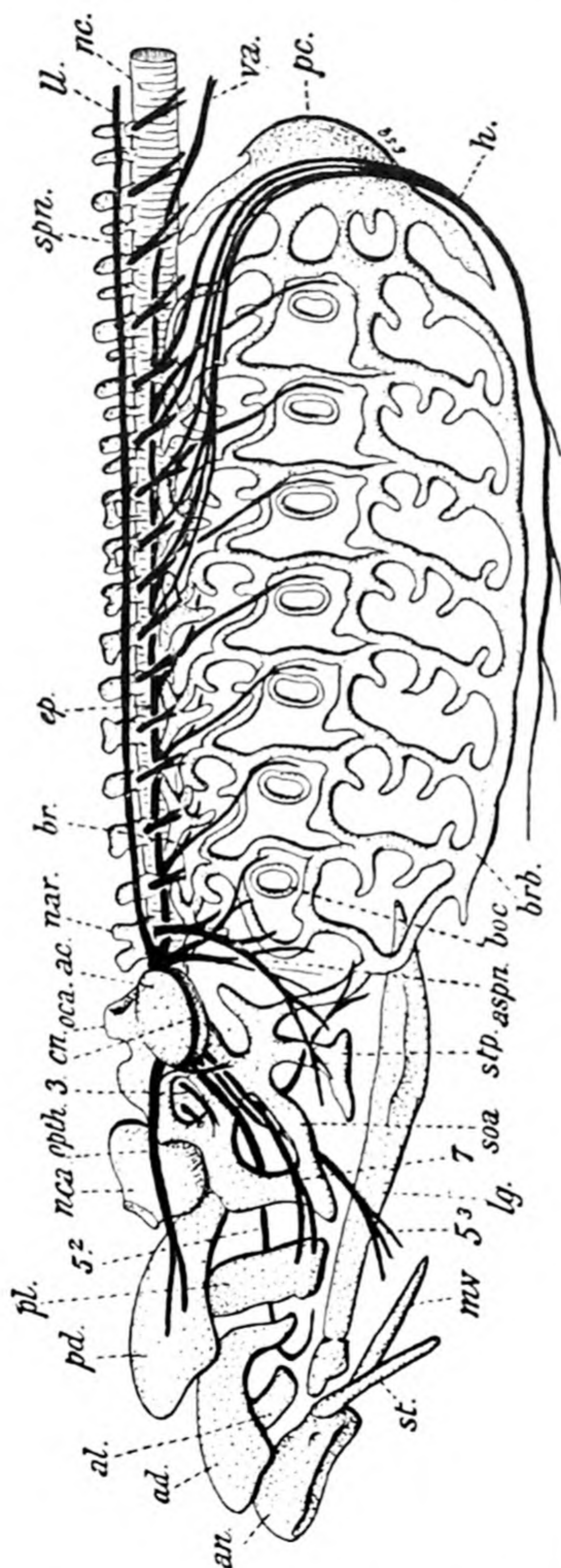
FIG. 743.

Petromyzon marinus, L. Skeleton of the anterior region with the cranial nerves and the ventral roots of the spinal nerves. *ac*, Auditory capsule; *ad*, anterior dorsal cartilage; *al*, anterior lateral; *an*, annular; *aspn*, combined anterior spinal nerves; *boc*, cartilage round the branchial opening; *br*, first branchial branch of vagus; *brb*, ventral cartilage of branchial basket; *cn*, connecting nerve from facial to vagus; *ep*, epibranchial branch of vagus running below spinal nerves; *h*, hypoglossal formed by combination of several spinal nerves; *lg*, lingual; *ll*, lateral-line branch of vagus; *mv*, median ventral; *nar*, neural arch; *nc*, notochord; *nca*, nasal capsule; *oca*, occipital arch; *opth*, superior ophthalmic nerve; *pc*, cartilaginous wall of pericardium; *pd*, posterior dorsal; *pl*, posterior lateral; *soa*, subocular arch; *spn*, ventral root of spinal nerve; *st*, styliform; *stp*, styliform process of subocular arch; *va*, visceral branch of vagus; 3, oculomotor nerve, with the optic nerve immediately in front; 5² and 5³, branches of trigeminal, and 7 of facial nerve. (From Goodrich, *Vert. Craniata*, 1909.)

branch of the vagus would then be a partial collector nerve. This explanation avoids the assumption that new central connexions have been established with the brain (Johnston, **359**). Moreover, the fact, otherwise difficult to account for, that the number of branchial branches of the vagus

corresponds to and varies with the number of branchial slits is naturally explained on the supposition that the process of ' collecting ' extends over all the segments of the region where branchial slits are developed ; neither excalation nor intercalation of nerves between the vagus and the first spinal need have taken place.

THE ' SYMPATHETIC ' NERVOUS SYSTEM

All the parts of the peripheral nervous system of a Vertebrate are so connected with each other and the central nervous system that it is not
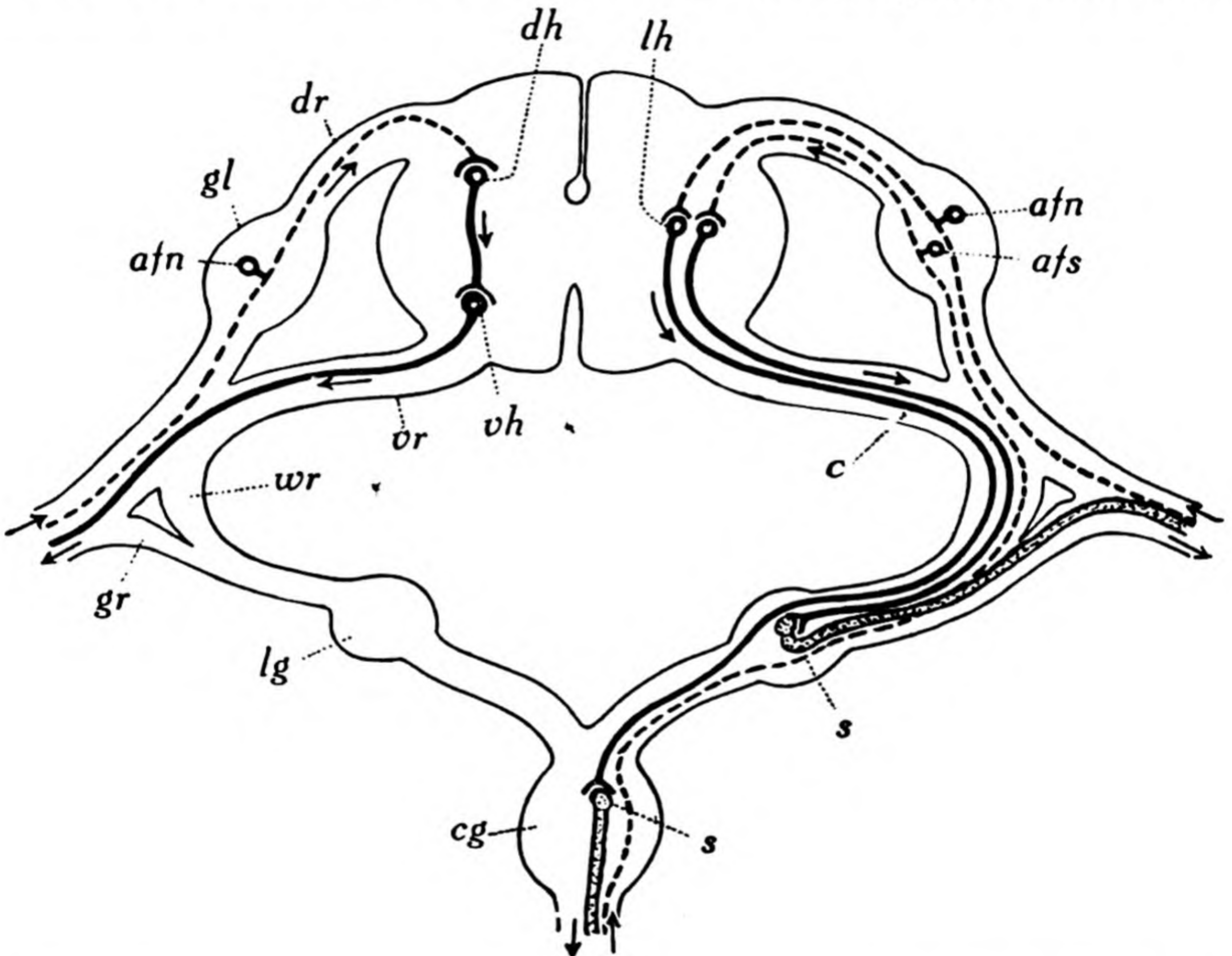
FIG. 744.

Reflex paths in peripheral nervous system. Diagram illustrating origin and distribution of nerve-fibres in trunk of Gnathostome (Mammal). Somatic reflex arc on left ; autonomic reflex arc on right. Afferent fibres represented as broken lines, efferent fibres as black lines ; sympathetic fibres red.* Arrows indicate course of nerve impulses. *afn*, Afferent sensory neuron ; *afs*, afferent neuron related to viscera ; *cg*, collateral sympathetic ganglion ; *dh*, intermediate neuron of dorsal horn ; *dr*, dorsal root ; *gl*, spinal ganglion ; *gr*, grey ramus ; *lg*, lateral sympathetic ganglion ; *lh*, preganglionic neuron of lateral horn related to sympathetic ; *s*, sympathetic neuron ; *vh*, motor neuron of ventral horn ; *vr*, ventral root ; *wr*, white ramus.
*Instead of red, stippled.

possible satisfactorily to subdivide it into anatomically separate regions. We may distinguish the central nervous system from the cranial and spinal nerves ; but if, with the anatomist, we define what remains when these have been removed as the 'sympathetic system', consisting of nerves, ganglia, and plexuses supplying chiefly unstriated muscles of the vascular

system, alimentary canal, and other viscera, and glands, we are met at once with the difficulty that many of the fibres coming from the sympathetic ganglia are distributed in the branches of the spinal and cranial nerves
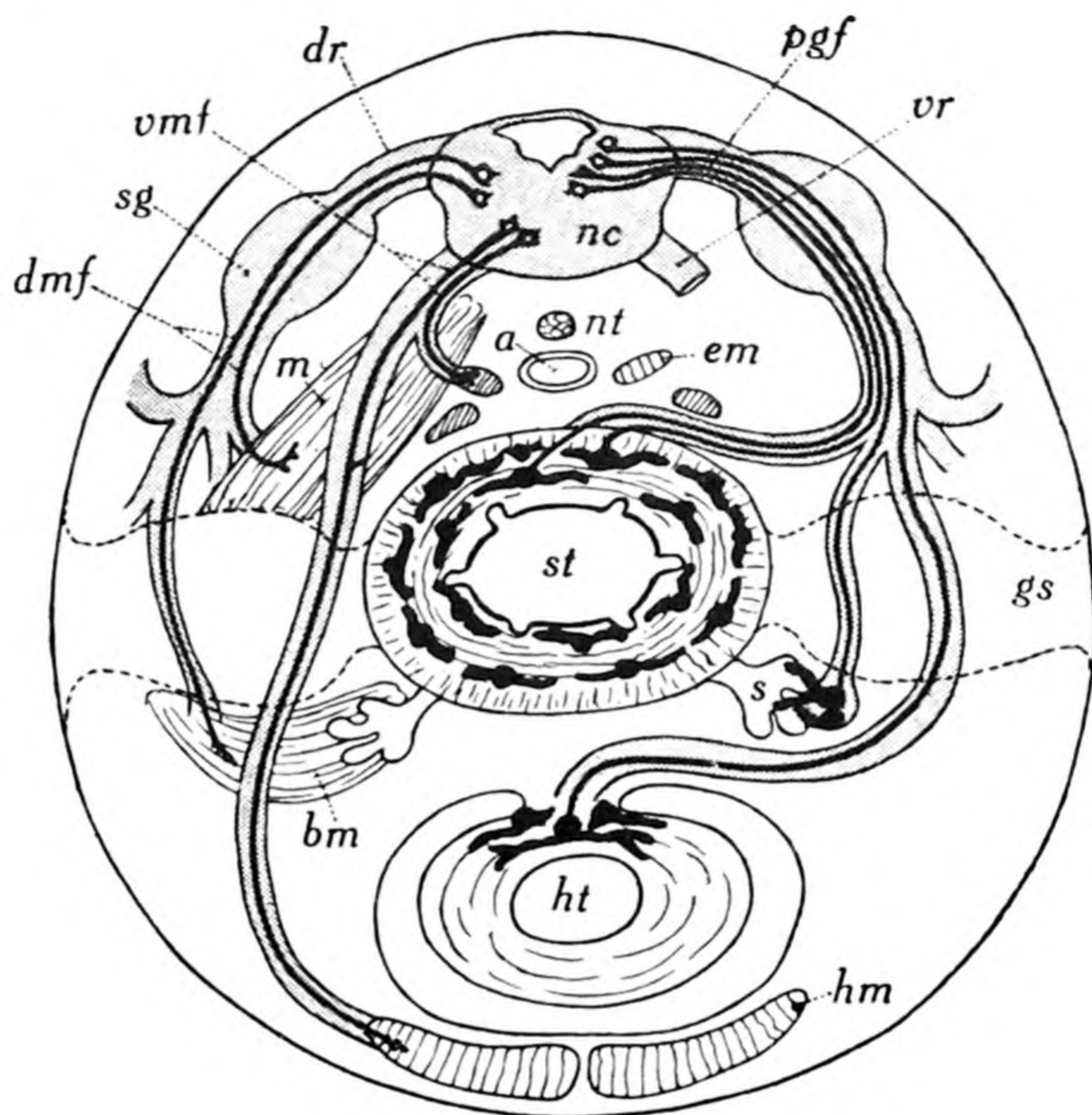
FIG. 745.

Efferent nervous system of head. Diagram of transverse section of branchial region of Gnathostome, showing distribution of excito-motor neurons in cranial nerves (black), and 'sympathetic' neurons (red).* a, Dorsal aorta ; bm, ventral branchial muscle ; dr, dorsal root ; dmf, dorsal motor fibres ; em, epibranchial muscle ; gs, position of gill-slit ; hm, hypobranchial muscle ; ht, heart ; m, dorsal branchial muscle ; nc, medulla ; nt, notochord ; pgf, connector preganglionic fibres ; s, salivary gland ; sg, segmental ganglion ; st, stomach ; vmf, ventral motor fibres ; vr, ventral root. Dorsal root nerve represents vagus, and ventral root nerve hypoglossal. em and hm, derived from segmented somites. bm and m from unsegmented lateral plate. 'Sympathetic' on right side.
*Instead of red, thick black lines.

to the skin, and indeed perhaps to all the muscles of the body both striated and smooth.[1] The time-honoured name sympathetic, then, used by the anatomist, indicates an arbitrarily distinguished portion of the peripheral

[1] A great deal of controversy has arisen of late years concerning the alleged double innervation of voluntary striated muscle fibres by both ordinary motor and autonomic nerve fibres. Thoracico-lumbar sympathetic fibres undoubtedly penetrate the muscles and are distributed in them, but whether they supply their own muscle fibres, fibres already provided with motor end plates, the blood-vessels, or a combination of these elements, is still uncertain (Peroncito, 1901; Boeke, 1913; Agduhr, 1920; Botezat, 1910; Kulchitsky, 1924; Hunter, 1925; also Wilson, 1921, for general review of the subject).

nervous system connected here and there with the cranial and spinal nerves. A better subdivision of the peripheral nerves can be made on functional grounds, taking into account the course of the nerve fibres serving as paths of impulses to and from the central nervous system (see p. 725).

The sympathetic of the anatomist contains many sensory afferent fibres from the viscera and internal organs ; but, since these differ in no essential from other afferent fibres, and since their cell-bodies are situated
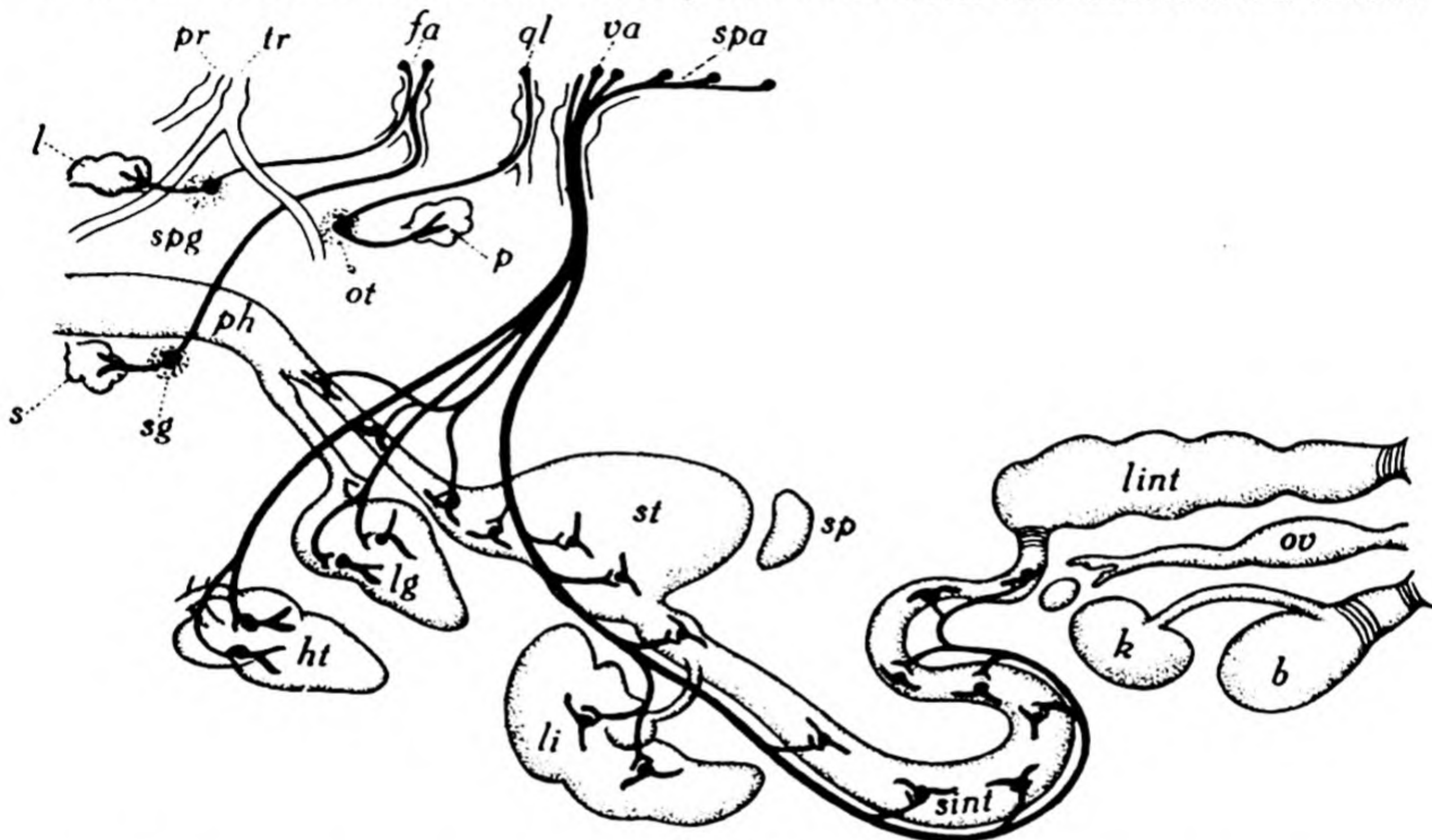
Fig. 746.

Diagram of Autonomic *dorsal root system* of *Mammal* (modified from W. H. Gaskell, 1916). *b*, Urinary bladder ; *fa*, facial nerve ; *gl*, glossopharyngeal ; *ht*, heart ; *k*, kidney ; *l*, lacrimal gland ; *lg*, lung ; *li*, liver ; *lint*, large intestine ; *ot*, otic ganglion ; *ov*, oviduct ; *p*, parotid gland ; *ph*, pharynx ; *pr*, profundus ; *s*, submaxillary gland ; *sg*, submaxillary ganglion ; *sint*, small intestine ; *sp*, spleen ; *spa*, spinal accessory ; *st*, stomach ; *tr*, trigeminal ; *va*, vagus.

in the dorsal root ganglia of the cranial and spinal nerves, they require no special treatment and can be set aside as the visceral sensory component of the peripheral nerves (p. 729).

To the whole efferent sympathetic system Gaskell gave the name ' involuntary ' since its action is usually not under the control of the will ; but Langley substituted the less objectionable name ' autonomic ', which is now generally used by physiologists (Gaskell, 1112 ; Langley, 1144 ; Müller, 1153 ; Huber, 1125). This autonomic system consists essentially of peripheral neurons, generally grouped in ganglia, receiving impulses from the central nervous system by branches of the cranial or spinal nerves, and carrying impulses by fibres distributed to practically all regions of the body, including the viscera. But the complete system

includes cells in the brain and spinal cord whose axons pass to the outer
ganglia or plexuses where they come into synaptic relation with other cells
whose axons supply the effector end organs (pigment cells, contractile cells
of blood-vessels and muscles, and gland cells). The peripheral cell may be
known as the sympathetic neuron, the central cell as the connector neuron.
The connector axon is known as the preganglionic fibre, the sympathetic
axon as the postganglionic fibre, Figs. 744-5, 750. In Gnathostomes,
whereas the preganglionic fibres are provided with the usual medullary
sheath, the postganglionic fibres remain non-myelenated, and can thus be
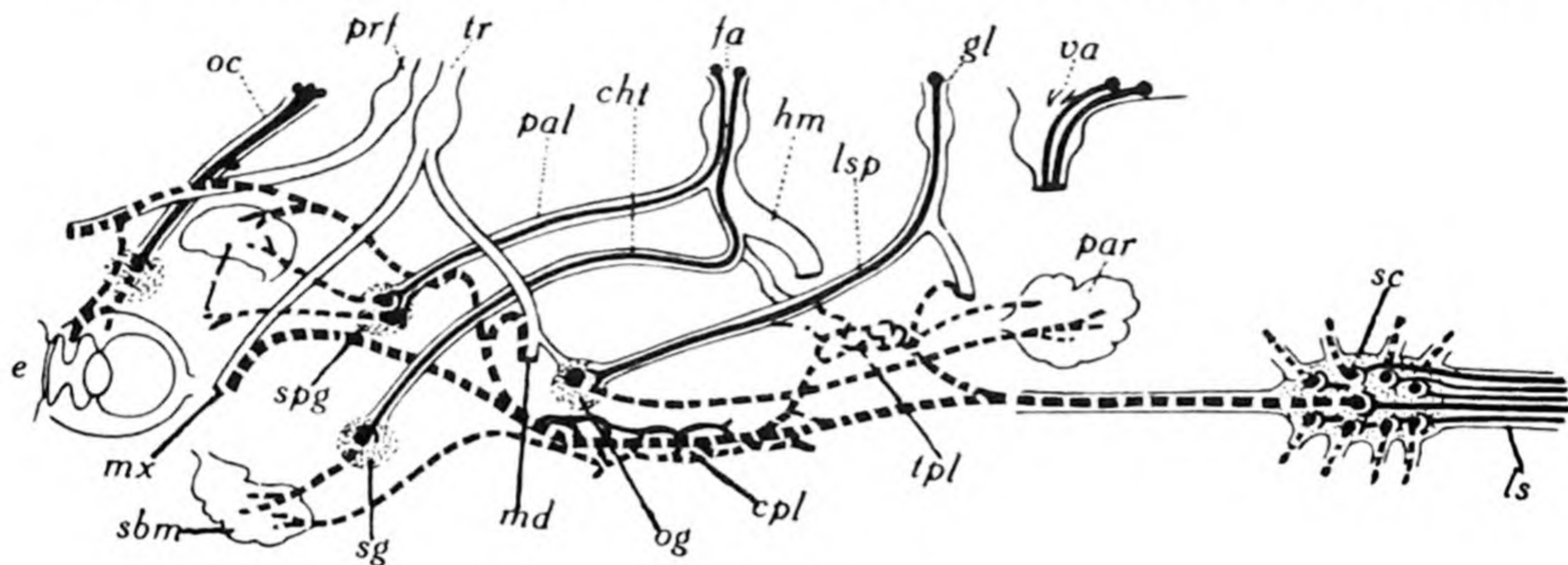
FIG. 747.

Diagram of *Autonomic supply in head* of Mammal ; left-side view of cranial nerves, etc. (modified
from Gaskell, 1916). Preganglionic neurons black ; postganglionic neurons red.* *cht*, Chorda tym-
pani ; *cpl*, carotid plexus ; *e*, eye ; *fa*, facial ; *gl*, glossopharyngeal ; *hm*, hyomandibular branch of
facial ; *l*, lacrimal gland ; *ls*, longitudinal sympathetic cord ; *lsp*, lesser superficial petrosal ; *md*,
mandibular branch ; *mx*, maxillary branch ; *oc*, oculomotor ; *og*, otic ganglion ; *pal*, palatine branch ;
par, parotid gland ; *prf*, profundus ; *sbm*, submaxillary gland ; *sc*, superior cervical ganglion ; *sg*,
submaxillary ganglion ; *spg*, sphenopalatine ganglion ; *tpl*, tympanic plexus ; *tr*, trigeminal ; *va*,
vagus.

*Instead of red, broken line.

distinguished ; moreover, except in the heart, the muscle fibres supplied
by sympathetic neurons are of the ' smooth ' unstriated kind.[1]

In the Gnathostomes there are paired ganglia in the head connected to
some of the cranial nerves ; paired segmental ganglia in the trunk and
anterior region of the tail, extending below the vertebral column on each
side, joined together by a longitudinal nerve trunk and connected to the
corresponding spinal nerves by rami communicantes ; also median ganglia
in the dorsal mesentery, and smaller peripheral ganglia distributed in the
viscera.

Except possibly in the enteric plexus, there are no short cuts peri-
pherally to sympathetic ganglia, and (neglecting possible ' axon reflexes ')
sympathetic reflex arcs can only be completed through the central nervous

[1] These distinctions, however, are not absolute, especially in lower forms.
For instance, in birds the postganglionic fibres to the iris muscles are medul-
lated, and these muscles are striated (Gaskell, 1112).

system to which all the sensory impulses are carried by afferent fibres whether by spinal, cranial, or visceral nerves.

Our modern knowledge of the detailed structure and function of the sympathetic nervous system is due chiefly to Gaskell and Langley ; and since it is best known in the higher vertebrates it will be well to begin by describing it in a Mammal.   The sympathetic neurons are connected
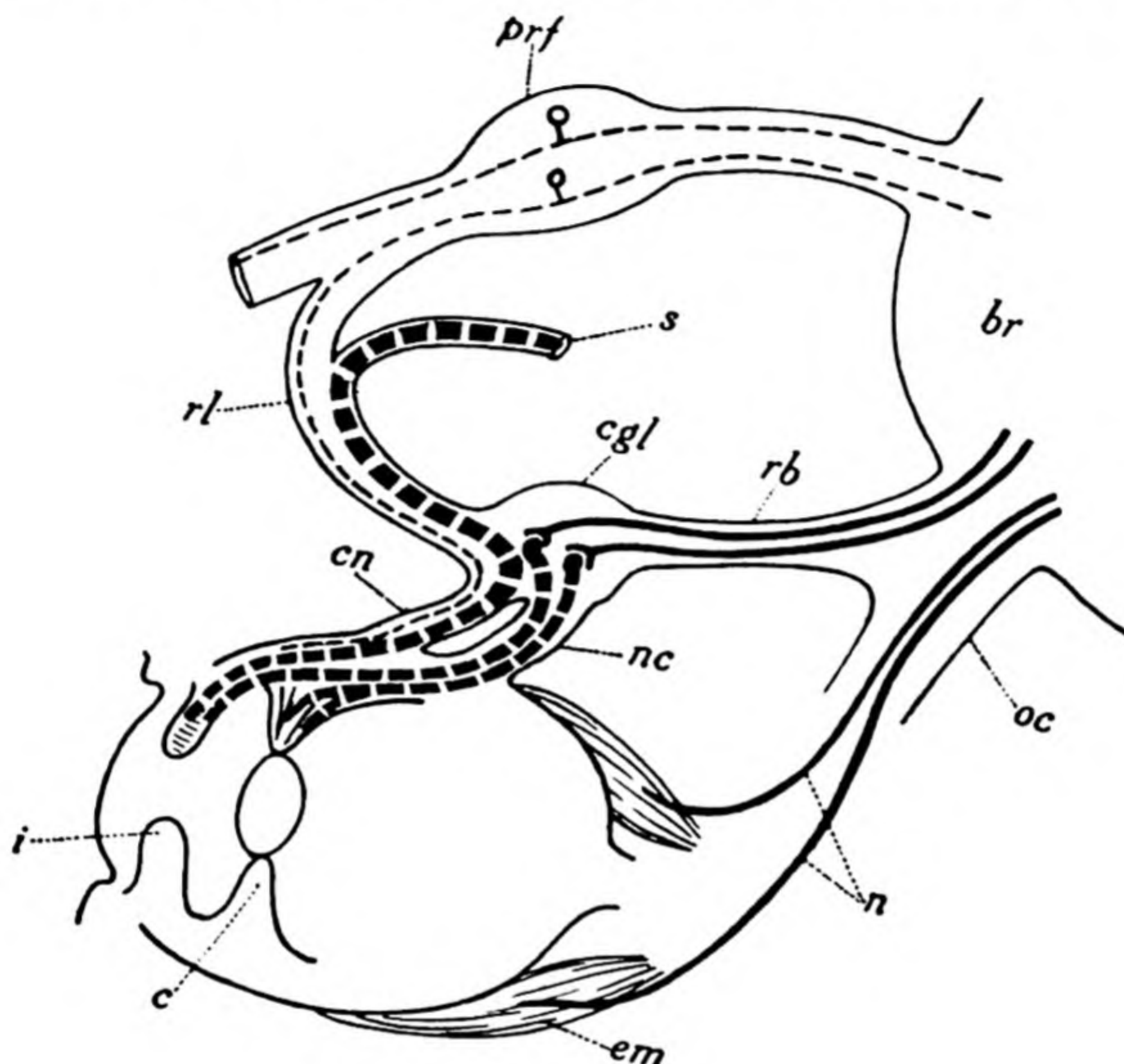
FIG. 748.

Diagram illustrating relation of dorsal cranial nerve (*prf*, profundus) and ventral cranial nerve (*oc*, oculomotor) with ciliary ganglion, *cgl*, and ' sympathetic '.   Afferent fibres broken lines ; efferent fibres black ; ' sympathetic ' fibres red.* *br*, Brain ; *c*, ciliary muscle ; *cn*, nerve, with sympathetic fibres to iris ; *em*, external eye-muscle ; *i*, iris muscle ; *n*, motor fibres ; *nc*, ciliary nerve, with sympathetic fibres to iris and ciliary muscle ; *rb*, radix brevis ; *rl*, radix longa ; *s*, sympathetic nerve from cervical ganglion.

*Instead of red, **thick** broken lines.

with the central nervous system by four ' outflows ' of preganglionic fibres :

(1) **The Mid-brain Outflow,** through the oculomotor nerve to the ciliary ganglion, supplies the iris sphincter and the ciliary muscle, Figs. 747-8-9.

(2) **The Bulbar** or **Hind-brain Outflow** through the facial, glosso-pharyngeal, and vagus nerves : through the 7th nerve to the spheno-palatine ganglion by the palatine or great superficial petrosal nerve supply-ing the lacrimal gland, and by the chorda tympani to the submaxillary gland; through the 9th to the otic ganglion supplying the parotid; through the 10th to sympathetic neurons in the heart (inhibitory), in the lungs, and

in the wall of the alimentary canal and its glands (including the liver) as far as the posterior end of the small intestine. It is these neurons of the alimentary canal which form the plexus of Auerbach (plexus myentericus) between the muscle layers, and the plexus of Meissner (plexus submucosus) near the mucous membrane of the stomach and small intestine, Figs. 745, 750 (see p. 782). Outflows (1) and (2) are related to cranial nerves and issue in front of the pectoral limb-plexus, Figs. 745-7.

(3) **The Thoracico-lumbar Outflow** is related to the spinal nerves between the pectoral and the pelvic limb-plexuses. The connector neurons, situated in the lateral column of the spinal cord, have axons which issue by the ventral spinal roots as medullated fibres which leave the mixed spinal nerves forming the white rami communicantes passing ventrally to a corresponding segmental series of vertebral or lateral ganglia on either side of the dorsal aorta. The vertebral ganglia are joined together by a longitudinal nerve trunk formed by the connector fibres and their collateral branches, and were originally no doubt distributed segmentally all along the body ; but they dwindle away in the tail, and in the cervical region run together to coalesce into a large superior and inferior ganglion still connected to the corresponding spinal nerves by segmental grey rami. Moreover the longitudinal nerve runs forward to connect with the cranial nerves and successive cranial sympathetic ganglia of outflows (1) and (2). From sympathetic neurons constituting all these lateral ganglia issue non-medullated fibres which pass as grey rami to the corresponding spinal nerves to supply the sweat-glands and smooth muscles of the skin (erector muscles of the hair, etc.) over the entire body. Sympathetic fibres also pass from the superior cervical ganglion to the radial ciliary muscle, the submaxillary gland (inhibitory), the buccal region, the larynx, the heart ; while the inferior cervical ganglion supplies the heart (accelerator) and larynx, Figs. 749 and 750.

More connector fibres pass out through the ventral thoracic roots and lateral ganglia into the median mesentery where they form the splanchnic nerves running to the unpaired prevertebral or collateral ganglia. Of these the most anterior, the coeliac, supplies the spleen, liver, and stomach; the superior mesenteric ganglion sends inhibitor fibres to the small intestine, and motor fibres to the ileo-caecal valve; from the most posterior ganglion, the inferior mesenteric, run fibres to the large intestine, the sphincter ani and sphincters of the urinary bladder and urethra, and muscles of the copulatory organs.

Lastly, a set of preganglionic connector fibres pass out still farther by the lumbar ventral roots and, running through the inferior mesenteric ganglion, join to a hypogastric nerve which branches to a plexus of

sympathetic neurons supplying the muscular and glandular walls of the excretory and genital ducts.

(4) **The Sacral Outflow** takes place behind the pelvic plexus by the ventral roots of the first three sacral nerves, where connector fibres pass out and join to a pelvic nerve (nervus erigens) which branches to a peripheral plexus in the wall of the large intestine, rectum, and bladder, and supplies the blood-vessels of the external copulatory organs, Fig. 750.
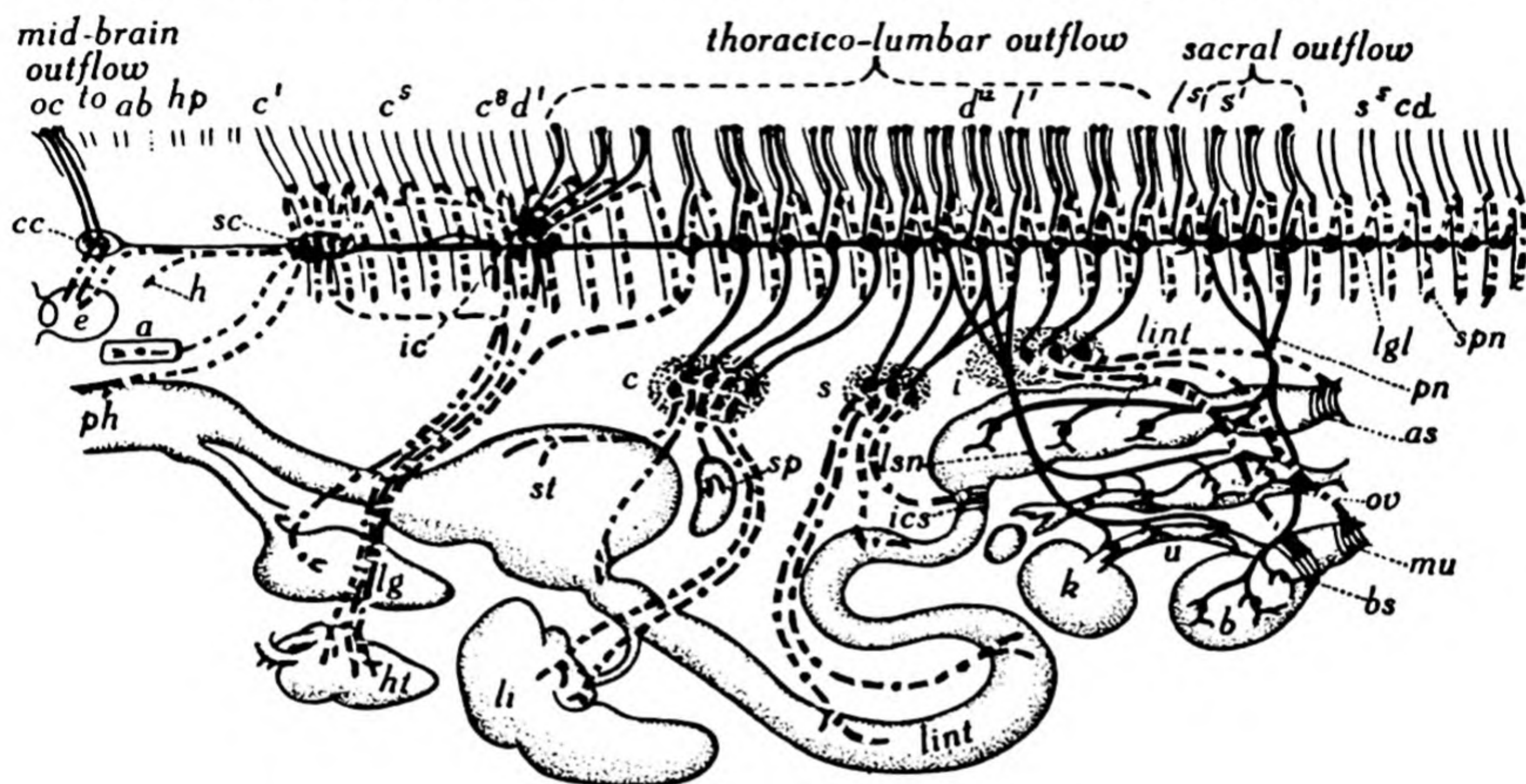
FIG. 749.

Diagram of Autonomic *ventral root system* of *Mammal* (modified from W. H. Gaskell, 1916). In black, preganglionic neurons of right side whose axons issue by ventral roots; in red, postganglionic neurons. *a*, Aorta; *ab*, abducens; *as*, anal sphincter; *bs*, bladder sphincter; *c*, semilunar ganglion; *cc*, ciliary ganglion; *e*, eye; *h*, branch to head; *i*, inferior mesenteric ganglion; *ic*, stellate ganglion; *lgl*, chain of lateral ganglia; *lsn*, lumbar splanchnic; *mu*, muscle of urethra; *pn*, pelvic nerve; *s*, superior mesenteric ganglion; *spn*, spinal nerve receiving sympathetic fibre from lateral chain by ramus communicans. Above are indicated ventral nerve roots from *oc*, oculomotor, anteriorly to fourth caudal posteriorly; *to*, trochlear; *ab*, abducens; *c*$^{1-8}$, cervical; *d*$^{1-12}$, dorsal or thoracic; *l*$^{1-5}$, lumbar; *s*$^{1-5}$, sacral; *c*^{1}, caudal. Other letters as in Fig. 746.

*Instead of red, broken lines.

From the above description it appears that in the Mammal the autonomic system has been subdivided by physiologists into four divisions or outflows from the central nervous system; but from the point of view of the comparative anatomist we may group these into two sets: (1) the dorsal root system comprising the outflow through the 7th, 9th, and 10th cranial nerves (and perhaps the nervus terminalis), and (2) the ventral root system comprising the outflows through the 3rd cranial nerve, the thoracico-lumbar and sacral nerves.

It is important to notice that an organ frequently receives a double autonomic supply, usually antagonistic. For instance the striated musculature of the heart receives accelerator impulses from the thoracic outflow and inhibitory impulses from the bulbar outflow, while the

reverse is the case with the unstriated musculature. The bulbar outflow stimulates in the intestine peristaltic action which is inhibited by the thoracic outflow. The secretion of the submaxillary gland is increased by impulses through the chorda tympani branch of the 7th nerve, but decreased by impulses from the superior cervical ganglion. In these instances one supply comes from the dorsal and the other from the ventral root system ; but in others the double supply may issue through the ventral
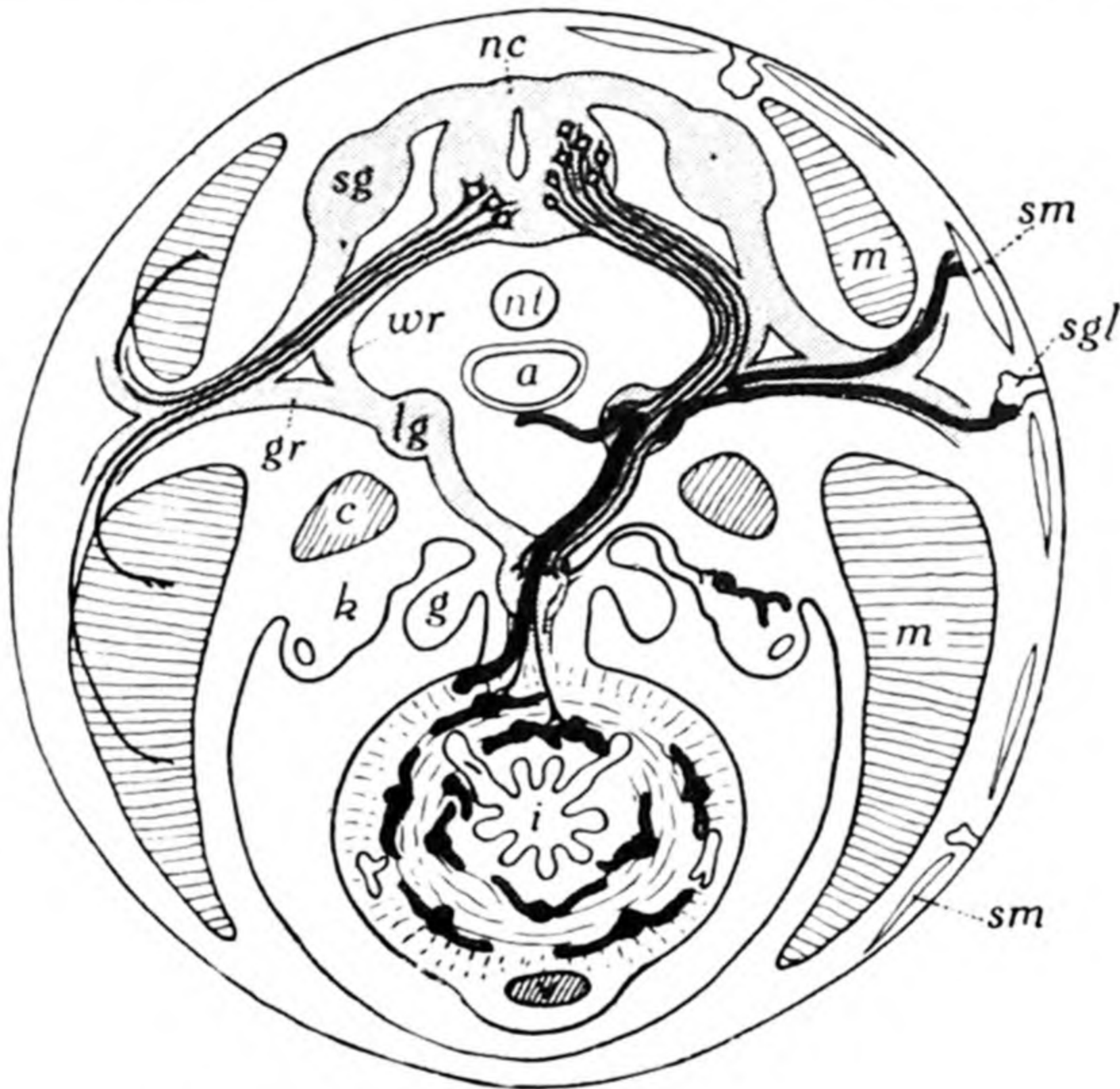
FIG. 750.

Efferent nervous system of trunk. Diagram of transverse section of trunk region of Gnathostome, showing distribution of excito-motor neurons in spinal nerve (black), and 'sympathetic' neurons (red). Compare Fig. 745. c, Cardinal vein ; g, gonad ; gr, grey ramus ; i, intestine ; lg, lateral ganglion (median collateral ganglion shown dorsal to intestine) ; m, myomere ; nc, spinal cord ; sgl, skin gland ; sm, smooth muscle ; wr, white ramus.

*Instead of red, thick black lines.

roots, as in the case of the large intestine, though here the antagonism may possibly be not of quite the same nature.

Another remarkable fact is that excitor fibres of the skin (erector muscles and glands) are distributed over segmental areas corresponding to the sensory areas of the mixed spinal nerves in the branches of which they run. But those supplying the greater part of the skin of the head pass forwards from the superior cervical ganglion into branches of the fifth nerve. Similarly vasomotor fibres may pass forwards and be distributed in the branches of the sensory cranial nerves.

Although the sympathetic system is by no means so well known in the lower Vertebrates as in Mammals, yet enough has been made out to

establish that it is built on the same general principle in all the Gnathostomes. That of Birds and Reptiles differs only in detail from that of the Mammal. Even in the Selachian (Chevrel, 1096 ; E. Müller, 1149) are found essentially the same chain of paired lateral ganglia, splanchnic nerves to unpaired collateral ganglia, and peripheral sympathetic neurons and plexuses in the alimentary canal and other viscera, all belonging to the ventral root system. A ciliary ganglion supplies the iris muscles. The dorsal root system is represented by nerves and ganglia connected with the 7th and 9th cranial nerves, as well as an extensive supply from the vagus to the stomach, small intestine, and other parts. Some Teleosts possess not only segmental lateral ganglia in the trunk, but also a ganglion to each of the sensory cranial nerves, all connected by a longitudinal cord (Allis, 402, 404), a condition possibly indicating a primitive stage in which segmental ganglia were regularly distributed along the whole body. In many Teleostomes, however, the system seems to be less definitely differentiated, the lateral ganglia less regular, and the sympathetic neurons scattered along the cardinal veins (Kuntz 1137)

In the Cyclostomes it is undoubtedly less well differentiated than in the typical Gnathostome. The sympathetic fibres are here no longer distinguishable by the absence of a medullary sheath, since no fibres in these lower Craniates have yet acquired such a sheath. The whole system is difficult to make out, and is but very imperfectly known, especially in the Myxinoids. The chain of lateral ganglia described by Julin in the larva has not been found by subsequent observers, nor are collateral ganglia known to occur ; but the thoracico-lumbar outflow seems to be represented by cells scattered along the cardinal veins, grouped near the segmental vessels and dorsal roots of the spinal nerves, where they are associated with chromafine cells distributed in almost all the segments of the body, and forming a mass on the sinus venosus (Giacomini, 1902-4 ; Fusari, 1889 ; Favaro, 1924). Moreover, V. Kupffer and Johnson have described sympathetic branches from the 7th and 10th cranial nerves to the pharyngeal region, and the vagus further supplies the whole of the alimentary canal. Here it is related to a plexus apparently representing Auerbach's plexus in the Gnathostomes (Dogiel, 1103 ; Smirnow ; Brandt, 1093 ; Tretjakoff, 1178).

No definite sympathetic system has been found in *Amphioxus*. Scattered ganglion cells have been described in the wall of its pharynx ; and such fibres as pass to the vascular system and alimentary canal come from visceral branches of the dorsal spinal roots, Fig. 707. In a general way these may represent the vagal supply of the Gnathostomes

(Fusari, 1889; Dogiel, 1104; Heymans and Stricht, v. d., 1122; Kutchin, 1141; Johnston, 1127 (see p. 782)).

Development and Phylogeny.—If we turn to embryology for a clue to the origin of the sympathetic system, we find that, whereas Remak and the early observers believed that it developed *in situ* from mesoblastic
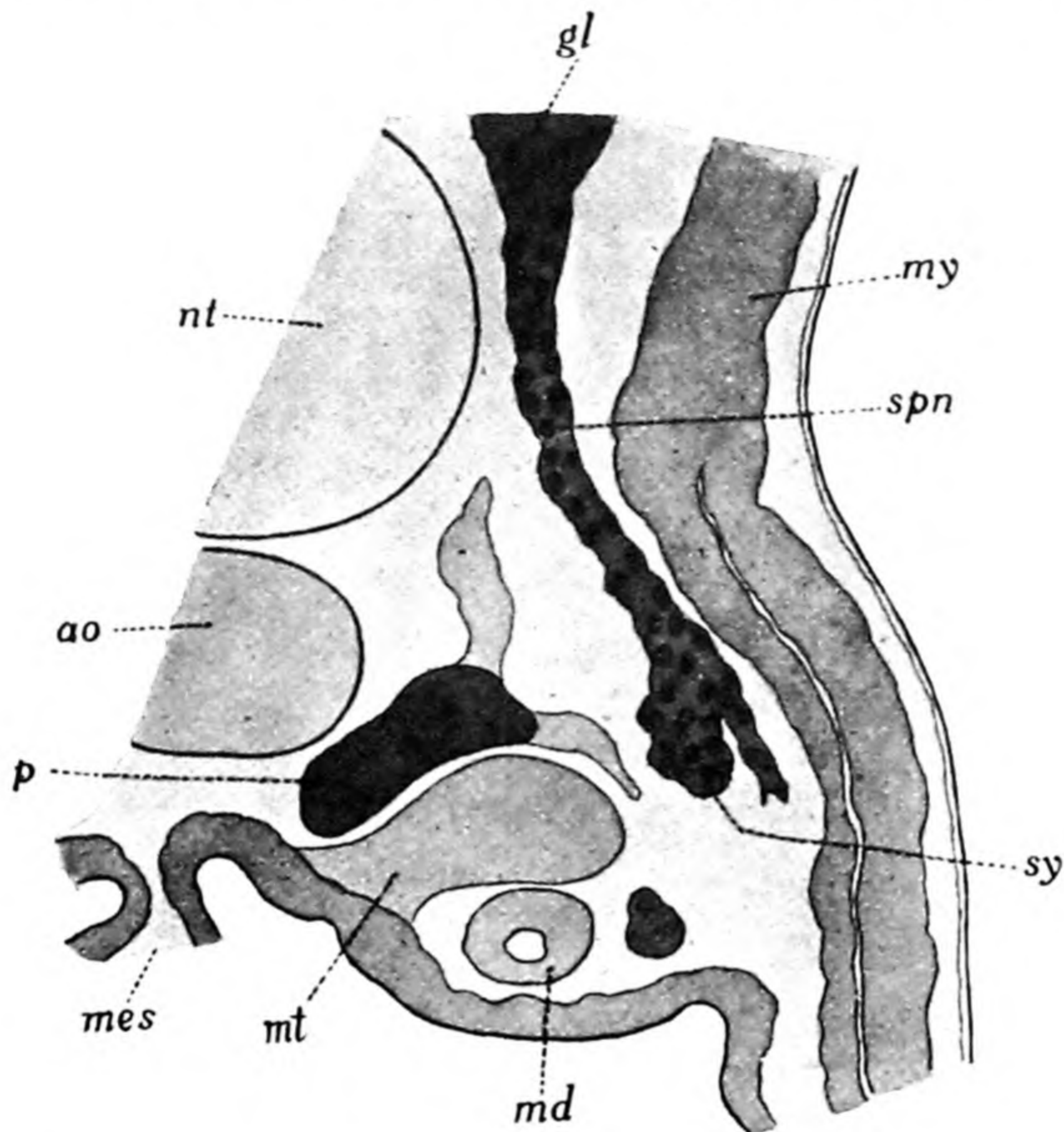
FIG. 751.

Scyllium canicula, embryo stage, L.   Portion of transverse section showing developing mesonephros and sympathetic system.   *mt*, Rudimentary mesonephric tubule not yet joined to duct, *md.*; *sy*, rudiment of sympathetic lateral ganglion from spinal nerve.

tissues, the modern and almost universally adopted view is that it is entirely of epiblastic origin.

Balfour in 1877 first established the epiblastic origin of the lateral ganglia in Selachians, showing that they develop from the mixed spinal nerves below the spinal ganglia as outgrowths which pass towards the aorta, Figs. 751-2.   In each segment the drawn-out connecting strand remains as the ramus communicans, while the longitudinal cord only develops later.   These observations were confirmed and extended by Onodi in 1886, who traced from the same source both lateral and collateral ganglia in Selachians and Lizards.   Similar views have been upheld by van Wijhe, 1889, Rabl, 1889, and Hoffmann, 1899, with regard to the Selachii, and since by others with regard to other groups of Gnathostomes,

Fig. 753 (Aves : Abel, 1077 ; Ganfini, 1110 ; Rau and Johnson, 1166). According to Schenk and Birdsall, 1878, the whole system in the body of the duck and mammal develops from the spinal ganglia. But it was His junior who first described in birds and mammals the whole system, including even the peripheral plexuses, as formed of epiblastic cells which actively
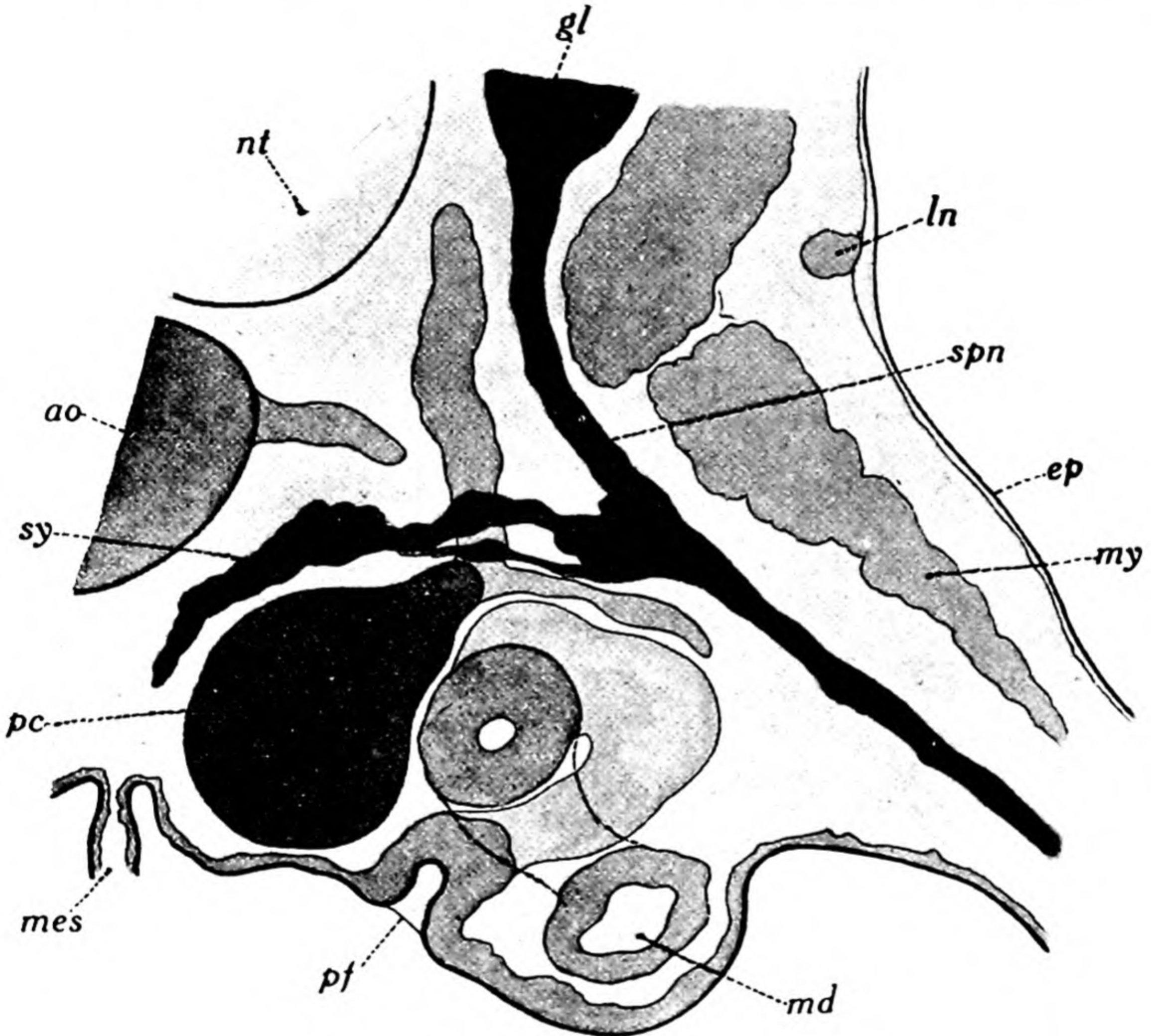
FIG. 752.

Scyllium canicula, embryo 23 mm. long, stage *M*. Portion of transverse section of anterior trunk segment showing developing mesonephros and sympathetic system. *ao*, Dorsal aorta ; *ep*, epidermis ; *gl*, spinal ganglion ; *ln*, lateral-line nerve ; *md*, mesonephric duct ; *mes*, mesentery ; *my*, myomere ; *nt*, notochord ; *pc*, posterior cardinal vein ; *pf*, peritoneal funnel ; *spn*, spinal nerve ; *sy*, rudiment of lateral ' vertebral ' sympathetic ganglion.

migrate from the neural tube to the spinal ganglia and thence farther and farther until they reach the remotest parts of the viscera. This active migration of independent cells into the mesenchyme towards the aorta seems to occur more in the higher than in the lower forms. Now, while many, like Held (1119), Marcus (1909), Kohn (1136), and E. Müller (1149, 1151), believe that the sympathetic cells migrate out through the dorsal root or are more directly produced from cells in the spinal ganglion, Froriep working on *Lepus* and *Torpedo*, and Cajal on the chick, maintain that

these motor neurons pass out from the neural tube by the ventral roots (Froriep; also Harrison in *Salmo*, '01, and Carpenter and Main, '07). Hoffmann and Neumayer, on the other hand, hold that both roots are concerned; Kuntz in a series of important studies on the development of the sympathetic in Pisces, Amphibia, Reptilia, Aves, and Mammalia (1137), maintains that in all these cells migrate from the neural tube by both the dorsal and the ventral roots, a conclusion also supported by Ganfini (1110). Kuntz made the important observation that the cells of the peripheral plexuses supplied by the vagus, including the myenteric and submucous plexuses, all pass out along the branches of the vagus which supply them. Certainly cells do migrate out by the ventral roots, and the only doubt is as to whether they are destined to develop into sympathetic neurons and not merely sheath-cells; but Kuntz seems to have set this doubt at rest by showing that, if the ventral region of the neural tube be removed in the chick embryo, the sympathetic fails to develop completely. By similar experiments on the frog, however, E. Müller claims to have shown that no neurons come from the ventral roots (1151).

The development of the cranial ganglia has been studied by Kuntz in man (1139) and by Stewart in the rat (1174). The otic ganglion is formed by cells migrating by the glossopharyngeal nerve, the submaxillary and sublingual ganglia of cells migrating by the chorda tympani, and the spheno-palatine of cells migrating by the palatine branch of the facial. These observations agree with the known course of the connector fibres. Kuntz, however, also describes a contribution to all three from the trigeminal ganglion. Moreover, the ciliary ganglion is said to be formed by cells migrating not only by the oculomotor nerve, but also by the profundus branch of the fifth nerve. Yet no connector fibres have been proved to be contained in this nerve.
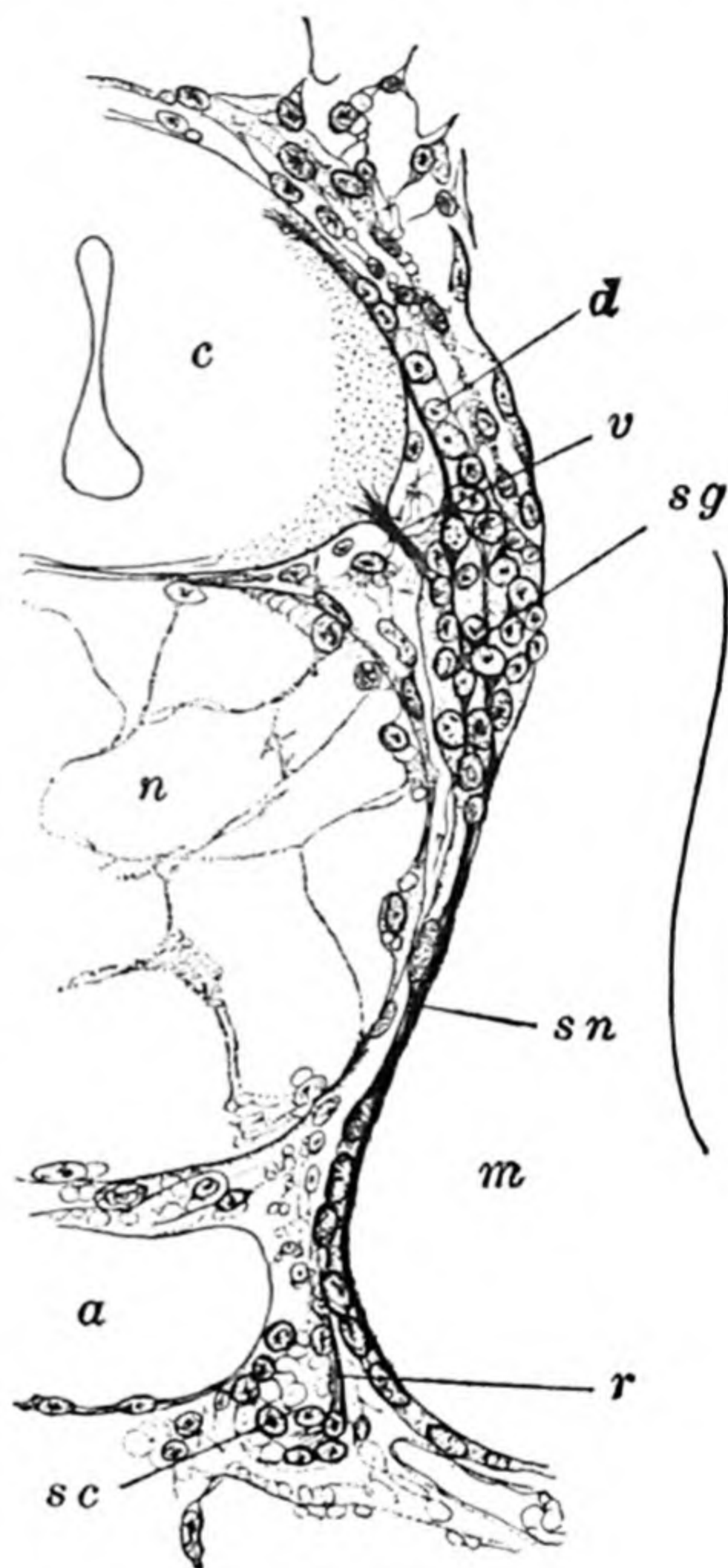
FIG. 753.

Transverse section through 8·6 mm. larva of *Rana esculenta*, illustrating relations of sympathetic cord and spinal nerve (after Held, from W. E. Kellicott, *Chordate Develt.*, 1913.) *a*, Dorsal aorta; *c*, spinal cord; *d*, dorsal (sensory afferent) root of spinal nerve; *m*, myotome; *n*, notochord; *r*, ramus communicans; *sc*, sympathetic cord; *sg*, spinal ganglion; *sn*, spinal nerve trunk; *v*, ventral (motor, efferent) root of spinal nerve.

The general result of these modern researches is that the sympathetic neurons are of epiblastic origin, and pass outwards in two main streams : one of cells of neural-tube or neural-crest origin which migrate through the dorsal roots and ganglia of the cranial and spinal nerves ; the other of cells from the lateral column of the central nervous system which migrate along the third cranial nerve and the ventral spinal roots. If these conclusions are correct it would follow that the emigrating cells may take the same course as the connector fibres in the adult. It is clear that this whole autonomic or ' sympathetic ' system might be defined as that part of the peripheral excitor nervous system whose special neurons are situated outside the central nervous system and segmental dorsal ganglia, and receive impulses through preganglionic fibres.

Gaskell long ago represented the whole efferent sympathetic system as formed by the outflowing of cells farther and farther from the central nervous system, with which they remain in connexion by correspondingly lengthening preganglionic connector fibres. Such indeed appears to be its ontogenetic development ; but it can scarcely be its phylogenetic history. For it cannot be held that the early Vertebrate had no efferent supply to its viscera, vascular system, skin muscles and glands. Rather may it be supposed that this peripheral nervous system, such as it occurs in Gnathostomes, has been differentiated out of a more diffuse general network, like that found in primitive Invertebrates, where the various efferent paths are imperfectly distinguished, and where the nerve fibres anastomose to a true network, perhaps not yet subdivided into neurons separated by synapses.

It may be suggested that in Vertebrates the central nervous system arose by the concentration of neurons originally distributed in such a diffuse network throughout the body ; and that the sympathetic system is composed of those excitor neurons which have not yet been so concentrated, but remain distributed at various points along the nerves and in the viscera. The history in phylogeny would then have been the reverse of what is believed to occur in ontogeny. But it must be confessed that the evidence for such a history is still far from satisfactory. A better knowledge of the structure, function, and development of the peripheral nervous system of the lower forms, more especially of the Cyclostomes, is urgently needed. A study of the peripheral nervous system in the Enteropneusta might also throw light on the early history of this system in the Vertebrata.

It is tempting to see the remains of a primitive network in the enteric plexus of Gnathostomes. The exact nature of this plexus is, however, by no means yet determined. A variety of cells have been described in it

(Dogiel, 1103; Cajal, 1893–4; Michailow; E. Müller, 1150, 1152; Kuntz, 1138; Hill, 1123), some of which have been held to be afferent, thus giving rise to reflex arcs within the wall of the gut; but this view has not been thoroughly established. Some authors describe the plexuses as composed of true networks (Bethe, 1903; E. Müller, 1149-50, 1152), while others describe them as made up of neurons separated by synapses (Cajal, 1911; Kuntz, 1138; Hill, 1123). According to E. Müller, in birds and mammals the myenteric plexus is formed of neurons related to vagal connector fibres, and the submucous plexus of a network related to fibres from the prevertebral ganglia; while in Selachians both would still be true networks.

The complex structure of the nerve plexuses of the intestine of Mammals may be briefly described as follows according to the latest work (C. J. Hill, 1123). The ganglia of the myenteric plexus of Auerbach and the submucous plexus of
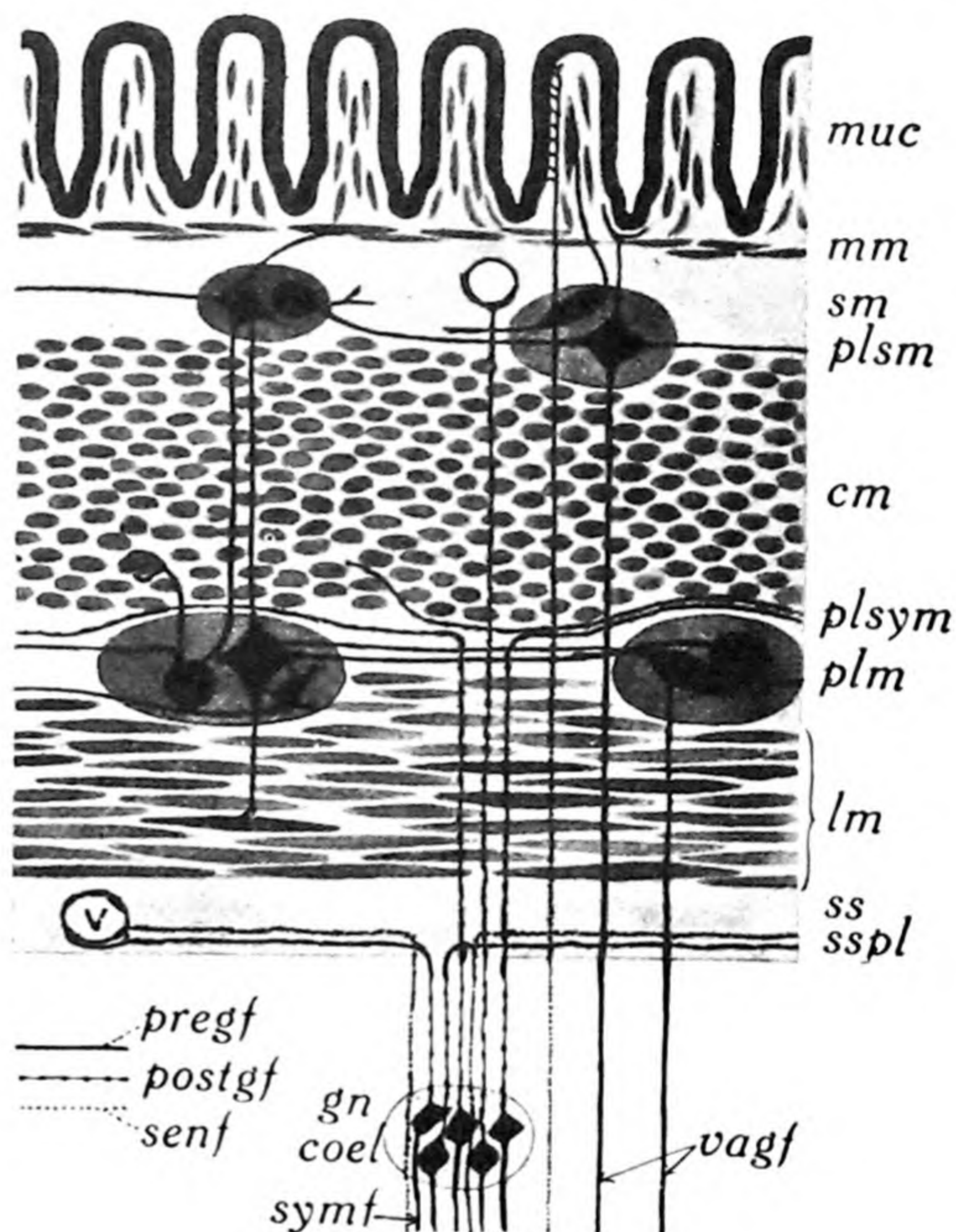
FIG. 754.

Diagram illustrating relations of nervous plexuses in wall of intestine of Mammal, seen in longitudinal section (from C. J. Hill, *Tr. Roy. Soc.*, 1927). *cm*, Circular muscle; *gn.coel*, coeliac ganglion; *lm*, longitudinal muscle; *mm*, muscularis mucosae; *muc*, mucosa with villi projecting into lumen; *plm*, myenteric plexus of Auerbach; *plsm*, submucous plexus of Meissner; *plsym*, sympathetic plexus; *sm*, submucosa; *ss*, subserosa; *sspl*, subserous plexus; *symf*, sympathetic fibres; *v*, blood-vessel; *vagf*, vagal fibres; *pregf*, preganglionic fibre; *postgf*, postganglionic fibre; *senf*, sensory fibre.

Meissner contain sympathetic neurons connected with preganglionic fibres of the vagus nerve. These sympathetic neurons may not only supply the muscles, but also send fibres to other neurons in neighbouring ganglia and from one plexus to the other. Both the outer coat of longitudinal muscles and the inner coat of circular muscles are supplied from the myenteric plexus. The submucous plexus supplies the thin innermost coat of muscles belonging to the mucosa and the muscles of the villi.

Postganglionic sympathetic fibres pass down the mesentery from the collateral ganglia to the intestine and are distributed chiefly to the blood-vessels and possibly to the muscle cells, Fig. 754.

Dorsal- and Ventral-root Systems.—An interesting and very important problem concerning the general morphology of the autonomic system remains to be discussed (Goodrich, 1927). Physiologists subdivide the whole system into (a) sympathetic proper or thoracico-lumbar outflow, and (b) parasympathetic (mid-brain, hind-brain, and sacral outflows). A third division, (c) enteric, is sometimes made for the plexuses of the alimentary canal. The division into sympathetic and parasympathetic may be justified on physiological grounds (action of drugs, etc.), but is not satisfactory from the point of view of morphology (p. 776).

What strikes the morphologist is that some of the outflows of pre-ganglionic fibres pass out through dorsal (posterior) nerve-roots, and others through ventral (anterior) nerve-roots. The whole system may be sub-divided into (a) the dorsal-root system (Hind-brain outflow, Figs. 745-6), and (b) the ventral-root system (Mid-brain, Thoracico-lumbar, and Sacral outflows, Figs. 749, 750).

The problem then arises : How has the latter system been evolved ? How have ' sympathetic ' neurons come to be connected with the central nervous system through ventral roots ? For the connexion through dorsal roots (as in the cranial nerves of the hind-brain) appears to be the primitive one.

In lower vertebrates, such as *Amphioxus* and *Petromyzon*, the ventral roots throughout the body supply the myomeres only, so far as we know. Any efferent fibres, belonging to or representing the ' sympathetic ' supply to the viscera or skin, must apparently in these forms pass out through the dorsal roots, not only in the head but throughout the whole length of the body. This condition persists in the hind-brain region of the higher forms, where the facial, glossopharyngeal, and vagus nerves represent the dorsal roots (of three segments), which remain separate from their corresponding ventral roots (abducens and hypoglossal; see above, pp. 216, 221, and 226).

Moreover, embryology seems to show that the hind-brain outflow of sympathetic cells is through dorsal-root cranial nerves, and although the evidence is still somewhat conflicting with regard to the thoracico-lumbar and sacral outflows these seem to take place also to some extent through the dorsal roots of the spinal nerves.

Clearly, the evidence as a whole points to the autonomic system having been originally related to the dorsal roots, and it remains to be explained how in the Gnathostomes sympathetic neurons belonging

to the mid-brain, thoracico-lumbar, and sacral outflows acquired a connexion with the central nervous system by means of preganglionic fibres issuing through the ventral roots. It can hardly be supposed that the whole ' ventral-root system ' is peculiar to and has arisen in the Gnathostome Vertebrates.

BIBLIOGRAPHY

CHAPTER I

Vertebral Column and Ribs and Sternum

1. **Albrecht, P.** Über d. Proatlas. *Zool. Anz.*, v. 3, 1880.
2. **Balfour, F. M.,** and **Parker, W. K.** On the Structure and Devel. of Lepidosteus. *Phil. Trans. R.S. London,* v. 173, 1882.
3. **Bardeen, C. R.** Devel. of Thoracic Vertebrae in Man. *Am. Jour. Anat.*, v. 4, 1905, and *Human Embryology*, 1910.
4. **Barge, J. A. J.** Entwickl. der Craniovertebralgrenze beim Schaf. *Anat. Hefte*, 1 Abt., v. 55, 1917.
5. **Baur, G.** Morph. der Wirbelsäule. *Biol. Centralbl.*, v. 6, 1886.
6. —— Proatlas. Atlas, and Axis of Crocodilia, *Amer. Nat.*, v. 20, 1886 ; Proatlas e. Schildkröte, *Anat. Anz.*, v. 10, 1895.
7. **Beer, G. R. de.** Devel. of Head in Heterodontus. *Quart. J. Micr. Sci.*, v. 68, 1924.
8. **Boeke, J.** Geldrollenstadium d. vertebraten Chorda. *Anat. Anz.*, v. 33, 1908.
9. **Brünauer, E.** Entwickl. d. Wirbelsäule b. d. Ringelnatter. *Arb. Zool. Inst. Wien*, v. 18, 1910.
10. **Budgett, J. S.** Structure of Larval Polypterus. *Trans. Zool. Soc.*, v. 16, 1902.
11. **Burlet, H. M. de.** Rudim. Wirbelkörper a. d. Spitze d. Dens epistrophei b. Bradypus. *Morph. Jahrb.*, v. 45, 1913 (Bibl.).
12. **Cope, E. D.** Rhachitomous Stegocephali and other papers. *Am. Nat.*, 1882–87.
13. —— Intercentrum of Terrestrial Vertebrata. *Trans. Amer. Phil. Soc.*, Philadelphia, v. 16, 1888.
14. **Cornet, Y.** Le prétendu proatlas des mammifères et de hatteria. *Bull. Ac. R. Belg.*, v. 15, 1888.
15. **Corning, H. K.** Neugliederung der Wirbelsäule, etc. *Morph. Jahrb.*, v. 17, 1891.
16. **Davison, A.** Devel. of Vert. Column and its Appendages (Amphiuma). *Anat. Anz.*, v. 14, 1897.
17. **Dean, B.** Chimaeroid Fishes. Carnegie Instit., Washington, 1906.
18. **Dollo.** Sur le Proatlas. *Zool. Jahrb.*, Abt. Anat., v. 3, 1889.
19. **Ebner, V. v.** Urwirbel u. Neugliederung der Wirbelsäule. *Sitz. Ak. Wiss. Wien*, v. 97, 1888 ; and v. 101, 1892.
20. —— Wirbel der Knochenfische u. die Chorda dorsalis der Fische u. Amphibien. *Sitz. Ak. Wiss. Wien*, v. 105, 1896.
21. **Field, H. H.** Bemerkungen über die Entwicklung der Wirbelsäule bei

der Amphibien ; nebst Schilderung eines abnormen Wirbelsegmentes. *Morph. Jahrb.*, v. 22, 1895, p. 340.

22. **Fortman, J. P. de G.** Entwickl. der Wirbelsäule von Megalobatrachus. *Tijdschr. Ned. Dierk. Ver.*, v. 16, 1918.

23. **Fritsch, A.** *Fauna der Gaskohle* . . . 4 vols. Prag., 1883–1901.

24. **Froriep, A.** Entwickl. der Wirbelsäule, insbes. des Atlas, Epistropheus, u. der Occipitalregion. *Arch. Anat. u. Phys.*, Anat. Abt., 1883 and 1886.

25. **Fürbringer, K.** Morph. d. Skeletes der Dipnoer, etc. *Denk. Med. Nat. Ges. Jena*, vol. 4, 1904.

26. **Gadow, H.** Evolution of Vertebral Column of Amphibia and Amniota. *Phil. Trans. R.S. London*, v. 187, 1896.

27. **Gadow, H.,** and **Abbott, E. C.** Evol. of Vertebral Column in Fishes. *Phil. Trans. R.S. London*, v. 186, 1895.

28. **Gaudry, A.** *Les Enchaînements du monde animal.* Paris, 1883.

29. **Gegenbaur, C.** *Vergl. Anat. der Wirbelsäule bei Amphibien u. Reptilien.* Leipzig, 1862.

30. —— Entw. der Wirbelsäule des Lepidosteus. *Jen. Zeitschr.*, v. 3, 1867.

31. **Goette, A.** Beitr. z. vergl. Morph. d. Skeletsystems. *Arch. f. mikr. Anat.*, v. 14, 1877 ; v. 15, 1878 ; v. 16, 1879.

32. —— *Entw. der Unke (Bombinator).* Leipzig, 1875.

33. —— Wirbelsystem. *Zool. Anz.*, v. 1, 1878 ; and v. 17, 1894.

34. —— Wirbelbau bei d. Reptilien. *Zeitschr. wiss. Zool.*, v. 62, 1897.

35. **Goodrich, E. S.** Vertebrata Craniata, *Treatise on Zoology*, Pt. 9. London, 1909.

36. —— On Scales of Fish. *Proc. Zool. Soc. London*, 1908 ; and. Bone of Fishes, *ibid.*, 1913.

37. **Grassi, B.** Entw. der Wirbelsäule der Teleostier. *Morph. Jahrb.*, v. 18, 1882.

38. **Hasse, C.** *Das naturl. Syst. d. Elasmobranchier.* 2 Parts and supplement. Jena, 1882–85.

39. —— Entwickl. d. Wirbelsäule : Triton. *Zeitschr. wiss. Zool.*, v. 53, 1892.

40. —— Elasmobranchier, Dipnoi. *Ibid.*, v. 55, 1893.

41. —— Ganoiden. *Ibid.*, v. 57, 1894.

42. —— Cyclostomen. *Ibid.*, v. 57, 1894.

43. **Hatschek, B.** Studien z. Segmenttheorie des Wirbeltierkopfes. *Morph. Jahrb.*, v. 40, 1910.

44. **Hatta, S.** Segmentation of Mesoblast in Petromyzon, etc. *Annot. Zool. Japan*, v. 4, 1901.

45. **Hay, O. P.** Vertebral Column of Amia. *Field Columb. Mus. Publ. Zool.*, v. 6, 1895.

46. **Hayek, H.** Proatlas u. Kopfgelenke b. Säugetieren. *Sitz. Ak. Wiss. Wien*, v. 130, 1923.

47. —— Schicksal d. Proatlas u. Entw. d. Kopfgelenke b. Reptilien u. Vögeln. *Morph. Jahrb.*, v. 53, 1924 (Bibl.).

48. **Higgins, G. M.** Devel. of Primitive Reptilian Vertebral Column (Alligator). *Am. J. Anat.*, v. 31, 1923.

49. **Howes, G. B.,** and **Swinnerton, H. H.** Devel. of Skeleton of Tuatara, Sphenodon punctatus. *Tr. Zool. Soc. London*, v. 16, 1901.

50. **Huene, F. v.** Phylog. Bedeutung des Wirbelbau der Tetrapoden. *Paläont. Zeitschr.*, v. 7, 1926.

51. **Jaekel, O.** Organisation von *Archegosaurus.* *Zeit. d. Deutsch. Geol. Ges.*, v. 48, 1896.

52. **Kapelkin, W.** Entwickl. des axialen Skeletts der Amphibien. *Bull. Soc. Nat. Moscou*, v. 14, 1900.

53. **Klaatsch, H.** Vergl. Anat. der Wirbelsäule: I. Urzustand der Fishwirbelsäule; II. Bildung knorpeliger Wirbelkörper bei Fischen; III. Phylogenese der Chordascheiden. *Morph. Jahrb.*, v. 19, 1893; v. 20, 1893; v. 22, 1895.

54. **Kölliker, A.** Unters. ü. d. Scheiden der Chorda dorsalis. *Verh. Phys.-med. Ges. Würzburg*, v. 9, 1859; v. 10, 1860; N.F., v. 3, 1872.

54a. —— *Ende d. Wirbelsäule d. Ganoiden*, etc., 1860.

55. **Kuppfer, C. von.** *Vergl. Entw. d. Kranioten.* I. Acipenser, 1893. II. and III. Petromyzon, 1894. München u. Leipzig.

56. **Lankester, E. R.** Contrib. to Knowledge of Amphioxus. *Quart. J. Micr. Sci.*, v. 29, 1889.

57. **Lotz, Th.** Bau der Schwanzwirbelsäule der Salmoniden, etc. *Zeitschr. f. wiss. Zool.*, v. 14, 1864.

58. **Lwoff, B.** Studien ü. d. Chorda u. Chordascheide. *Bull. Soc. Nat. Moscou*, 1887.

59. **Macallister, A.** Devel. and Variation of Atlas. *J. of Anat. and Physiol.*, v. 27, 1893; Devel. and Variation of Second Cervical Vertebra. *Ibid.*, v. 28, 1894.

60. **Männer, H.** Entw. d. Wirbelsäule b. Reptilien. *Zeitschr. f. wiss. Zool.*, v. 66, 1899.

61. **Männich, H.** Entwickl. der Wirbelsäule v. Eudyptes. *Jen. Zeitschr.*, v. 37, 1903.

62. **Marcus, H., u. Blume, W.** Wirbel u. Rippen bei Hypogeophis. *Zeitschr. f. Anat. u. Entw.*, v. 80, 1926.

63. **Marshall, W.** Bau der Vögel. *Naturw. Bibl. Leipzig*, 1895.

64. **Murray, J. A.** Vert. Column of Primitive Urodela. *Anat. Anz.*, v. 13, 1897.

65. **Osborn, H. F.** Intercentra and Hypapophyses in Mosasaurs, Lizards, and Sphenodon. *Amer. Nat.*, v. 34, 1900.

66. **Parker, T. J.** Anat. and Devel. of Apteryx. *Phil. Trans. R.S. London*, v. 182, 1891; v. 183, 1892.

67. **Parker, W. K.** Skeleton of the Marsipobranch Fishes. *Phil. Trans. R.S.*, v. 174, 1883.

68. **Peter, K.** Wirbelsäule der Gymnophionen. *Ber. Nat. Ges. Freiburg*, v. 9, 1895.

69. —— Bedeutung des Atlas der Amphibien. *Anat. Anz.*, v. 10, 1895 (Bibl.).

70. **Piiper, J.** Evolution of Vertebral Column in Birds. *Phil. Trans. R.S.* B. v. 216, 1928.

71, 72. **Rabl, C.** Theorie d. Mesoderms. *Morph. Jahrb.*, v. 15, 1889; v. 19, 1892.

73. **Rabinerson, A.** Vergl. Anat. der Wirbelsäule der Knorpelfische. *Anat. Anz.*, 59, 1925.

74. **Ridewood, W. G.** Devel. of Vertebral Column in Pipa and Xenopus. *Anat. Anz.*, v. 13, 1897, p. 359.

75. —— Caudal Diplospondyly of Sharks. *J. Linn. Soc. Zool.*, v. 27, 1899.

76. —— Calcification of Vertebral Centra in Sharks and Rays. *Phil. Trans. R.S. London*, v. 210, B., 1921.

77. **Rosenberg, E.** Entw. der Wirbelsäule des Menschen. *Morph. Jahrb.*, v. 1, 1875.

78. Schauinsland, H.   Entw. d. Wirbelsäule nebst Rippen u. Brustbein. *Hertwigs Handb. Entw. Wirbeltiere*, v. 3, Jena, 1906 (Bibl.).

79. Scheel, C.   Entw. der Teleostierwirbelsäule. *Morph. Jahrb.*, v. 20, 1893.

80. Schmidt, L.   Wirbelbaues von Amia Calva. *Zeitschr. f. wiss. Zool.*, v. 54, 1892.

81. Schneider, A.   *Beitr. z. vergl. Anat. der Wirbeltiere*, Berlin, 1879.

82. Schultze, O.   Embryonale u. bleibende Segmentierung. *Verh. Anat. Ges.*, Berlin, 1896.

83. Schwarz, H.   Morphogenie der Wirbelsäule. *Sitzb. Ges. Nat. Fr.*, Berlin, 1908 ; *Paläontogr.* v. 21, 1908.

84. Sečerov, S.   Entstehung der Diplospondylie der Selachier. *Arb. Zool. Inst. Wien*, v. 19, 1911.

85. Shufeldt, R. W.   Osteology of Amia Calva. *Rep. U.S. Com. of Fish and Fisheries* (1883), 1885.

86. Sunier, A. L. J.   Différentiation interne du Myotome, etc. *Tijdschr. Nederl. Dierk. Ver.*, v. 12, 1911.

87. Tretjakoff, D.   Wirbelsäule des Neunauges. *Anat. Anz.*, v. 61, 1914.

88. —— Chordascheide u. Wirbel bei Zyklostomen u. Fische. *Zeitschr. Zellf. u. mikr. Anat.*, v. 4, 1924.

89. —— Chordascheiden der Urodelen. *Z. Zellforsch. u. mikr. Anat.*, v. 5, 1927.

90. Ussow, S.   Anat. u. Entwickl. der Wirbelsäule der Teleostier. *Bull. Soc. Imp. Nat. Moscou*, 1900.

91. Weiss, A.   Entwickl. d. Wirbelsäule d. Ratte. *Z. wiss. Zool.*, v. 69, 1901.

92. Wieland, G. R.   Terminology of Vertebral Centra. *Am. Journ. of Sci.*, v. 8, 1899.

93. Wijhe, J. W. v.   Entwickl. des Kopf- und Rumpfskeletts von Acanthias. *Bijdr. tot de Dierk.*, Amsterdam, 1922.

94. Willey, A.   *Amphioxus and Ancestry of Vertebrates*, 1894.

95. Williston, S. W.   *Osteology of Reptiles*. Harvard U.P., 1925.

96. Welcker, H.   Bau u. Entw. der Wirbelsäule. *Zool. Anz.*, v. 1, 1878.

97. Woodland, W. N. F.   Caudal Anatomy and Regeneration in Gecko. *Quart. J. Micr. Sci.*, v. 65, 1920.

98. Zittel, K. A.   *Handbuch den Paläontologie*, v. 3 (Pisces, Amphibia, Reptilia, Aves), v. 4 (Mammalia), Munich, 1887, and later translations (Bibl.).

99. Zykoff, W.   Knorpels der Chorda bei Siredon. *Bull. Soc. Nat. Moscou*, 1893.

RIBS AND STERNUM

100. Baur, G.   Morphology of Ribs. *Amer. Nat.*, v. 21, 1887.

101. —— Morph. of Ribs and Fate of Actinosts in Fishes. *J. of Morph.*, v. 3, 1889.

102. —— Rippen u. ähnliche Gebilde. *Anat. Anz.*, v. 9, 1894.

103. Boulenger, G. A.   On the Nature of ' Haematophyses '. *Ann. Mag. Nat. Hist.*, v. 12, 1893.

104. Dollo, L.   Sur la morph. des côtes. *Bull. sc. de la France et Belgique*, v. 24, 1892 ; Sur la morph. de la colonne vertébrale. *Ibid.*, v. 25, 1893.

105. Gamble, D. L.   Morph. of Ribs and Transv. Processes in Necturus. *J. Morph.*, v. 36, 1922.

106. Göppert, E.   Kenntniss der Amphibienrippen. *Morph. Jahrb.*, v. 22, 1895.

107. —— Unters. z. Morph. der Fischrippen. *Morph. Jahrb.*, v. 23, 1895.

108. **Göppert, E.** Morph. der Amphibienrippen. *Gegenbaur Festschr.*, 1, 1896.

109. **Hatschek, B.** Rippen der Wirbeltiere. *Verh. Anat. Ges.*, Berlin, 1889.

110. **Hoffmann, C. K.** Morphologie der Rippen. *Niederl. Archiv. Zool.*, v. 4, 1878.

111. **Knickmeyer, C.** *Entwickl. der Rippen bei Triton*, Munich, 1891.

112. **Mayerhofer, F.** Morph. u. Entwickl. der Rippensystems der Urodelen. *Arb. Zool. Inst. Wien*, v. 17, 1909.

112a. **Paterson, A. M.** Sternum, devel. etc. *J. Anat. and Phys.*, v. 35, 1901.

112b. **Ruge, G.** Entw. a. Brustbein. *Morph. Jahrb.*, v. 18, 1880.

113 **Parker, T. J.** Origin of the Sternum. *Trans. New Zeal. Inst.*, v. 23, 1891.

114. **Schöne, G.** Befestigungen der Rippen an der Wirbelsäule. *Morph. Jahrb.*, v. 31, 1902.

115. **Whitehead, R. H.**, and **Waddell, J. A.** Early Devel. of Mammalian Sternum. *Am. Jour. Anat.*, v. 12, 1911.

CHAPTER II

MEDIAN FINS

116. **Balfour, F. M.**, and **Parker, W. K.** Structure and Devel. of Lepidosteus. *Phil. Trans. R.S. London*, v. 173, 1882.

117. **Breder, C. M.** Locomotion of Fishes. *Zoologica, N.Y. Zool. Soc.*, v. 4, 1926.

118. **Bridge, T. W.** Mesial Fins of Ganoids and Teleosts. *J. Linn. Soc. Zool.*, v. 25, 1896.

119. **Dollo, L.** Sur la phylogénie des dipneustes. *Bull. Soc. Belge Géol.*, v. 9, 1895.

120. —— Éthologie paléont. relative aux poissons. *Bull. Soc. Belge Géol. et Pal.*, v. 20.

121. **Emery, C.** Fierasfer. *Fauna u. Flora d. Golfes v. Neapel*, Monogr. 2, 1880.

122. **Goodrich, E. S.** Dermal Fin-rays of Fishes. *Q. Journ. Micr. Sci.*, v. 47, 1903.

123. **Gregory, W. K.** Orders of Teleostomous Fishes. *Ann. N.Y. Acad. Sci.*, v. 17, 1907.

124. **Hatschek, B.** Schichtenbau von Amphioxus. *Anat. Anz.*, v. 3, 1888.

125. **Huxley, T. H.** Devel. of some Parts of Skeleton of Fishes. *Q. Journ. Micr. Sci.*, v. 7, 1859.

126. **Kiaer, J.** Downtonian Fauna of Norway : I. Anaspida. *Vidensk. Skr. Mat. Naturw. Kl.*, 1924.

127. **Kirkaldy, J. W.** Genera and Species of Branchiostomidae. *Quart. J. Micr. Sci.*, v. 37, 1895.

128. **Mayer, P.** Unpaaren Flossen der Selachier. *Mitth. Zool. Sta. Neapel*, v. 6, 1885.

129. **Regan, C. T.** Caudal Fin of Elopidae. *Ann. Mag. Nat. Hist.*, ser. 8, v. 5, 1910.

130. **Ryder, J. A.** Origin of Heterocercy and Evol. of Fins and Fin-rays of Fishes. *U.S. Com. of Fish. Report for 1884*, 1886.

131. **Salensky, W.** Entw. der unpaaren Flossen der störartigen Fische. *Ann. Mus. Zool. Ac. Imp. St-Pétersbourg*, 1899.

132. **Schaffer, J.** Bau u. Entw. des Schwanzflossenknorpels von Petromyzon. *Anat. Anz.*, 19, 1901.

133. **Schmalhausen, J. J.** Morph. der unpaaren Flossen : I. Entwickl. *Zeitschr. wiss. Zool.*, vol. 100, 1912 ; II. Bau u. Phylogenese. *Ibid.*, vol. 104, 1913.

134. **Stensiö, E. A. S.** Triassic Fishes from Spitzbergen : II. Saurichthyidae. *K. Svenska Vet.-Akad. Handlingar*, v. 2, 1925.

135. —— Downtonian and Devonian Vertebrates of Spitzbergen (Cephalaspidae). *Norske Videnskaps-Akad. Oslo*, No. 12, 1927.

136. **Totton, A. K.** Struct. and Devel. of Caudal Skel. of Pleurogramma. *Proc. Zool. Soc. London*, 1914.

137, 138. **Traquair, R. H.** Palaeospondylus Gunni. *Proc. Roy. Phys. Soc. Edinburgh*, v. 12, 1893 ; *Proc. Zool. Soc.*, 1897.

139. **Whitehouse, R. H.** Caudal Fin of Teleostomi. *Proc. Zool. Soc. London*, 1910.

139. —— Caudal Fin of Fishes. *Proc. Roy. Soc.*, London, B, v. 82, 1910.

140. —— Evol. of Caudal Fin. *Rec. Ind. Mus.*, v. 15, 1918.

CHAPTER III

PAIRED FINS

141. **Agar, W. E.** Devel. of Ant. Mesoderm and Paired Fins in Lepidosiren and Protopterus. *Trans. Roy. Soc. Edinburgh*, vol. xlv., 1907.

142. **Balfour, F. M.** Devel. of Skeleton of Paired Fins of Elasmobranchs. *Proc. Zool. Soc.*, 1881.

143. **Bateson, W.** *Materials for Study of Variation*, London, 1894.

144. **Braus, H.** Innervation der paarigen Extremitäten bei Selachiern. *Jen. Zeitschr.*, v. 29, 1895.

145. —— Entwickl. der Muskulatur u. des periph. Nervensyst. d. Selachier : I. Teil, Die metotischen Urwirbel ; II. Teil, Die paarigen Gliedmassen. *Morph. Jahrb.*, v. 27, 1899.

146. —— Versteinerter Gliedmassenknorpel von Selachiern. *Verh. Phys. Med. Ges. Würzburg*, 34, 1901.

147. —— Muskeln u. Nerven der Ceratodusflosse. *Zool. Forsch. Denkschr. Med. Nat. Ges.*, Jena, 1901.

148. —— Entw. d. Form der Extremitäten u. d. Extremitätenskelets. *Hertwigs Handb. Entw. Wirbeltiere*, v. 3, Jena, 1906.

148a. —— Segmentalstruct. d. mot. Nervenplexus. *Anat. Anz.*, v. 34.

149. **Brongniart, C.** Pleuracanthus Gaudryi. *Bull. Soc. Géol. de France*, v. 16, 1888.

150. **Broom, R.** Origin of Cheiropterygium. *Bull. Am. Mus. N.H.*, v. 32, 1913.

151. **Bunge, A.** Biserial Archipterygium bei Selachiern u. Dipnoern. *Jen. Zeitschr. f. Naturw.*, v. 8, 1874.

152. **Cope, E. D.** Homologies of Fins of Fishes. *Am. Nat.*, v. 24, 1890.

152a. —— On Symmorium. *Amer. Natur.*, v. 27, 1893.

153. **Davidoff, M. v.** Vergl. Anatomie der hinteren Gliedmasse der Fische : Pt. I. *Morph. Jahrb.*, 5, 1879 ; Pt. II. *Morph. Jahrb.*, 6, 1880 ; Pt. III. *Morph. Jahrb.*, 9, 1883.

154. **Dean, B.** Morph. of Cladoselache. *Journ. Morph.*, v. 9, 1894 ; *Trans. N. York Acad. Sci.*, v. 13, 1894.

155. —— *Fishes Living and Fossil*, New York, 1895 (Bibl.).

156. **Dean, B.** Fin-fold Origin of Paired Limbs, in Light of Ptychopterygia of Palaeozoic Sharks. *Anat. Anz.*, v. 11, 1896.

157. **Derjugin, K.** Bau u. Entwickl. d. Schultergürtels u. d. Brustflossen b. d. Teleostiern. *Zeitschr. wiss. Zool.*, v. 96, 1910.

158. **Döderlein, L.** Skelet v. Pleuracanthus. *Zool. Anz.*, v. 12, 1889.

159. **Dohrn, A.** Paarigen u. unpaaren Flossen der Selachier. *Mitt. Zool. Sta. Neapel*, v. 5,, 1884.

159a. —— Unpaare Flosse, u. d. Reste der Beckenflosse bei Petromyzon, *Mitt. Zool. Sta. Neapel*, v. 6, 1885.

160. **Ducret, E.** Dével. des membres pairs et impairs des téleostéens. *Trutta Inaug. Diss.*, Lausanne, 1894.

161. **Frechkop, S.** Struct. et dével. de l'organe copulateur des raies. *Arch. de Biol.*, v. 35, 1925.

162. **Fürbringer, M.** Lehre v. den Umbildungen der Nervenplexus. *Morph. Jahrb.*, v. 5, 1879.

163. —— *Unters. z. Morph. u. System der Vögel*, Jena, 1888.

164. —— Über d. spino-occipitalen Nerven. *Festschr. z. Geb. C. Gegenbaur*, v. 3, 1897.

165. **Gadow, H.** Myologie d. hinteren Extremitäten der Reptilien. *Morph. Jahrb.*, v. 7, 1881.

166. **Gegenbaur, C.** *Unters. z. vergl. Anat. d. Wirbeltiere*, Leipzig, Heft 1, 1864 ; Heft 2, 1865 ; Heft 3, 1872.

167. —— Skelet der Gliedmassen in allgemein und der Hintergliedmassen der Selachier insbesondere; Skelet der Hintergl. bei der Männchen der *Selachier* und *Chimären*. *Jen. Zeit. Med. u. Naturw.*, v. 5, 1870.

168. —— Ueber das Archipterygium. *Jen. Zeit. Med. Nat.*, v. 7, 1873. Flossenskelet der Crossopterygier u. Archipterygium. *Morph. Jahrb.*, v. 22, 1895.

169. —— Morph. der Gliedmaassen der Wirbelthiere. *Morph. Jahrb.*, v. 2, 1876.

170. —— *Vergl. Anatomie der Wirbeltiere*. 2 vols. Leipzig, 1898.

171. **Goodrich, E. S.** On the Pelvic Girdle and Fin of Eusthenopteron. *Quart. J. Micr. Sci.*, v. 45, 1901.

172. —— Devel., etc., of the Fins of Fish. *Quart. J. Micr. Sci.*, v. 50, 1906.

173. —— Segmental Struct. of Motor Nerve-plexus. *Anat. Anz.*, v. 36, 1910.

173a. —— Metameric Segmentation and Homology. *Quart. J. Micr. Sci.*, v. 59, 1913.

174. **Gregory, W. K., Miner, R. W.,** and **Noble, G. K.** Carpus of Eryops and Primitive Cheiropterygium. *Bull. Am. Mus. N.H.*, v. 48, 1923.

175. **Guitel, F.** Dével. des nageoires paires du Cyclopterus lumpus. *Arch. Zool. Expér.*, v. 4, 1896.

176. **Haller, B.** Schultergürtel der Teleostier. *Arch. mikr. Anat.*, v. 67, 1905.

177. **Hamburger, R.** Paarigen Extremitäten von Squalus, Trigla, Periophthalmus u. Lophius. *Rev. Suisse de Zool.*, 12, 1904.

178. **Hammarsten, O. D.** Innervation d. Bauchflossen b. d. Teleostiern. *Morph. Jahrb.*, v. 42, 1911.

179. **Harrison, R. G.** Entw. der Flossen der Teleostier. *Arch. f. mikr. Anat.*, v. 46, 1895.

180. **Haswell, W. A.** Paired Fins of Ceratodus. *Proc. Linn. Soc. N.S. Wales*, v. 7, 1883.

181. —— Elasmobranch Skeleton. *Ibid.*, v. 9, 1885.

182. **Herringham, W. P.**　Minute Anat. of Brachial Plexus.　*Proc. Roy. Soc. London*, v. 41, 1886.

183. **Howes, G. B.**　Skeleton and Affinities of Paired Fins of Ceratodus. *Proc. Zool. Soc. London*, 1887.

184. —— Pectoral Fin-Skeleton of Living Batoid Fishes and of Extinct Squaloraja.　*Proc. Zool. Soc. London*, 1890.

185. **Huber, O.**　Kopulationsglieder der Selachier.　*Z. wiss. Zool.*, v. 70, 1901.

186. **Jaekel, O.**　Ü. d. Organisation der Pleuracanthiden.　*Sitz. Ges. naturf. Fr. Berlin*, 1895.

187. **Jhering, H. v.**　Das *periphere Nervensystem der Wirbelthiere*, Leipzig, 1878.

188. **Jungersen, H. F. E.**　Bauchflossenanhänge der Selachiermännchen. *Anat. Anz.*, v. 14, 1898.

189. —— Appendices Genit. in Greenland Shark, Somniosus, etc.　*Danish Ingolf Exped.*, v. 2, Copenhagen, 1899.

190. **Kiaer, J.**　Downtonian Fauna of Norway: I. Anaspida.　*Videnskaps. Skr. Mat. naturw. Kl.*, 1924.

191. —— Mouth of oldest known Vertebrates.　*Palaeobiologica*, v. 1, 1928.

192. **Klaatsch, H.**　Brustflosse der Crossopterygier.　*Festschr. f. C. Gegenbaur*, Leipzig, 1896.

193. **Kryzanovsky, S.**　Entwickl. d. paarigen Flossen bei Acipenser, Amia u. Lepidosteus.　*Acta Zool.*, v. 8, 1927.

194. **Lankester, E. R.**　The Cephalaspidae (and Pteraspidae).　*Mon. Palaeontogr. Soc.*, 1868–70.

195. **Lebedinsky, N. G.**　Entwickl.-mech. Unters. an Amphibien, II.　*Arb. Vergl. Anat. Inst. Lettl. Univ.*, Riga, 1925.

195a. **Leigh-Sharpe, W. H.**　Sec. Sexual Char. of Elasmobranchs.　*J. of Morph. and Phys.*, v. 34, 1920 ; v. 35, 1921 ; v. 39, 1924.

196. **Mivart, St. G.**　On Fins of Elasmobranchs.　*Trans. Zool. Soc. London*, v. 10, 1879.

197. **Mollier, S.**　Die paarigen Extremitäten der Wirbeltiere: I. Das Ichthyopterygium.　*Anat. Hefte*, Abt. 1, v. 3, 1893.

197a. —— Die paarigen Extremitäten der Wirbeltiere : II. Das Cheiropterygium.　*Anat. Hefte*, Abt. 1, v. 5. 1894–95.

198. —— Entw. d. paar. Flossen des Störs.　*Anat. Hefte*, Abt. 1, v. 8, 1897.

199. **Müller, E.**　Brustflosse der Selachier.　*Anat. Hefte*, v. 39, 1909.

200. —— Muskeln u. Nerven der Brustflosse bei Acanthias.　*Ibid.*, v. 43, 1911.

201. —— Anat. u. Entwickl. des peripheren Nervensystems b. d. Selachiern. *Arch. mikr. Anat.*, v. 81, 1913.

202. **Osburn, R. C.**　Origin of the Paired Limbs of Vertebrates.　*Am. J. Anatomy*, v. 7, 1907.

203. **Paterson, A. M.**　Position of Mammalian Limb.　*J. Anat. and Phys.*, v. 23, 1889.

204. —— Origin and Distrib. of Nerves of Lower Limb.　*Ibid.*, v. 28, 1893.

205. **Petronievics, B.**　Pectoral Fin of Eusthenopteron.　*Ann. Mag. Nat. Hist.*, v. 2, 1918.

206. **Rabl, C.**　Ursprung der Extremitäten.　*Zeitschr. wiss. Zool.*, v. 70, 1901.

207. **Rautenfeld, E. v.**　Skelett der hinteren Gliedmassen von Ganoiden und Teleostiern.　*Inaug. Diss.*, Dorpat, 1882 ; and *Morph. Jahrb.*, v. 9, 1884.

208. **Regan, C. T.**　Phylogeny of Teleostomi.　*Ann. Mag. Nat. Hist.*, v. 13, 1904.

209. **Rosenberg, E.**　Entwickl. der Wirbelsäule, etc.　*Morph. Jahrb.*, v. 1, 1875.

210. **Rosenberg, E.** Modus des Zustandekommens der Regionen a. d. Wirbelsäule des Menschen. *Ibid.*, v. 36, 1907.

211. **Ruge, E.** Entw. d. Skelettes d. Extremität v. *Spinax niger. Morph. Jahrb.*, vol. 30, 1902.

212. **Ruge, G.** Verschiebungen i. d. Endgebieten der Nerven des Plexus lumbalis. *Morph. Jahrb.*, v. 20, 1893.

213. **Salensky, W.** Dével. de l'ichthyoptérygie des poissons ganoides et dipnoides. *Ann. Mus. Zool. Ac. Imp. St-Pétersbourg*, v. 3, 1898.

214. **Semon, R.** Entw. d. paarigen Flossen der Ceratodus. *Denkschr. Med. Nat. Ges. Jena*, v. 4, 1898.

215. **Sewertzoff, A. N.** Entwickl. d. Muskeln, etc., d. Extremitäten d. niederen Tetrapoda. *Bull. Soc. Imp. Nat. Moscou*, 1907.

215. —— Dével. des extrémités de Chamaeleo. *Jour. Russe de Zool.*, v. 1, 1916.

216. —— Devel. of Pelvic Fins of Acipenser. *J. Morph. and Physiol.*, v. 41, 1926.

217. —— Morph. d. Brustflossen d. Fische. *Jen. Zeitschr. f. Naturw.*, v. 62, 1926.

218. **Stensiö, E. A. S.** *Triassic Fishes from Spitzbergen*, Vienna, 1921.

219. **Thacher, J. K.** Median and Paired Fins. *Trans. Connecticut Acad.*, v. 3, 1877; Ventral Fins of Ganoids. *Ibid.*, v. 4, 1878.

220. **Traquair, R. H.** Structure and Affinities of Tristichopterus alatus. *Trans. Roy. Soc. Edinburgh*, v. 27, 1874.

221. —— Lower Devonian Fishes of Gemünden. *Trans. Roy. Soc. Edinburgh*, v. 40, 1893; Supplement. *Ibid.*, v. 41, 1895.

222. —— On Cladodus Neilsoni. *Trans. Geol. Soc. Glasgow*, v. 11, 1897.

223. —— On Thelodus Pagei, from Old Red Sandstone of Forfarshire. *Trans. Roy. Soc. Edinburgh*, v. 39, 1898.

223a. —— Fossil Fishes . . . in Silurian Rocks of South of Scotland. *Trans. Roy. Soc. Edinburgh*, v. 39, 1898.

224. —— Devonian Fishes of Campbeltown and Scaumenac Bay. *Geol. Mag.*, v. 7, 1890; v. 10, 1893.

225. —— Drepanaspis Gemündenensis. *Geol. Mag.*, v. 7, 1900; v. 9, 1902.

226. **Vogel, K.** Entw. d. Schultergürtels u. d. Brustflossen Skelettes der Forelle (Trutta). *Jena. Zeitschr. Naturw.*, v. 45, 1909.

227. **Watson, D. M. S.** Cheiropterygium. *Geol. Mag.*, D. 6, v. 1, 1914.

228. **Welker, H.** Bau u. Entwickl. der Wirbelsäule. *Zool. Anz.*, v. 1, 1878.

229. **Whiteaves, J. F.** Fossil Fishes of Devonian Rocks of Canada. *Trans. Roy. Soc. Canada*, v. 4, 1887; and v. 6, 1888.

230. **Wiedersheim, R.** *Gliedmassenskelet der Wirbeltiere*, Jena, 1892.

231. **Woodward, A. Smith.** *Outlines of Vertebrate Palaeontology* Cambridge, 1898 (Bibl.),

CHAPTER IV

PECTORAL AND PELVIC GIRDLES

232. **Andrews, C. W.** Devel. of Shoulder Girdle in Plesiosaur. *Ann. Mag. Nat. Hist.*, v. 15, 1895.

233. —— *Cat. of Marine Reptiles of Oxford Clay.* 2 Pts. London, 1910–13.

234. **Anthony, R.** Morph. of the Shoulder Girdle. 17th Internat. Cong. Med., 1913.

235. **Anthony, R., et Vallois H.** Ceinture scapulaire chez les Batraciens. *Bibl. Anat.*, v. 24, 1914.

236. **Baur, G.** Pelvis of Testudinata, etc. *Jour. Morph.*, v. 4, 1891.

237. **Bogoljubsky, S.** Brustbein etc. b. e. Lacertiliern. *Zeitschr. wiss. Zool.*, v. 110, 1914.

238. **Braus, H.** Brustschulterapparat der Froschlurche. *Sitzb. d. Heidelberger Akad. d. Wiss.*, 1919.

239. **Broom, R.** Sterno-Coracoidal Articulation in a Foetal Marsupial. *J. Anat. and Phys.*, v. 31, 1899. Devel. and Morph. of Marsupial Shoulder Girdle. *Trans. Roy. Soc. Edinb.*, v. 39, 1900.

239a. —— Structure of Mesosaurus. *Trans. S. Afr. Phil. Soc.*, v. 15, 1904.

240. —— Lacertilian Shoulder Girdle. Devel. of App. Skel. of Ostrich. *Trans. S. Afr. Philos. Soc.*, v. 16, 1906.

241. —— Morphology of Coracoid. *Anat. Anz.*, v. 41, 1912.

242. **Bunge, A. v.** *Entwickl. des Beckens der Amphibien, Reptilien u. Vögel.* Dorpat, 1880.

243. **Cope, E. D.** Shoulder Girdle and Extremities of Eryops. *Trans. Am. Phil. Soc.*, v. 16, 1890.

244. —— Degenerate Types of Scapular and Pelvic Arches in Lacertilia. *J. Morph.*, v. 7, 1892.

245. **Eggeling, H.** Morph. des Manubrium Sterni. *Festschr. z. E. Haeckel*, 1904.

245. —— Clavicula, etc. *Anat. Anz.*, v. 29, 1906.

246. **Eisler, P.** Homologie der Extremitäten. *Abh. naturf. Ges. Halle*, v. 19, 1893–95.

247. **Fraas, E.** *Ichthyosaurier d. süddeutschen Trias u. Jura.* Tübingen, 1891.

248. **Fraas, O.** Pterodactylus suevicus. *Palaeontographica*, v. 25, 1878.

249. **Fuchs, H.** Entw. u. vergl. Anat. des Brustschultergürtels der Wirbeltiere: 1. Clavicula bei Talpa etc. *Zeitschr. f. Morph. u. Anthrop.*, 1912. 2. Schultergürtel der Amphibia anura. *Ibid.*, v. 22, 1922. 3. *Ibid.*, v. 24, 1924. 5. (Cartilago procoracoidea, etc.). *Anat. Anz.*, 61, 1926. 6. (Praezonales etc.). *Verh. Anat. Ges. Freiburg*, 1926. 7. Amphibien, Sauriern u. Testudinaten. *Anat. Anz.*, 64, 1927.

250. **Fürbringer, M.** Vergl. Anat. des Brustschulterapparates. *Jen. Zeitschr.*, v. 7, 1873; v. 8, 1874; v. 34, 1900; v. 36, 1902.

250. —— *Morph. Jahrb.*, v. 1, 1875.

251. **Gegenbaur, C.** Clavicula u. Cleithrum. *Morph. Jahrb.*, v. 23, 1895.

252. **Gelderen, C. van.** Devel. of Shoulder Girdle and Episternum in Reptiles. *Proc. Kon. Acad. v. Wet. Amsterdam*, v. 26, 1923.

253. —— Entw. des Brustschulterapparats bei Sauriern. *Anat. Anz.*, v. 59, 1925.

254. **Goette, A.** Morph. des Skelettsystems der Wirbeltiere: Brustbein u. Schultergürtel. *Arch. mikr. Anat.*, v. 14, 1877.

255. **Goodrich, E. S.** Pectoral Girdle in young Clupeids. *J. Linn. Soc. London, Zool.*, v. 34, 1922.

256. **Gregory, W. K.** Origin of Birds. *Ann. N. York Ac. Sci.*, v. 27, 1916.

256a. **Gregory, W. K., and Camp, C. L.** Comp. Myology and Osteology. *Bull. Am. Mus. N.H.*, v. 38, 1918.

257. **Hanson, F. B.** Ontogeny and Phylogeny of the Sternum. *Am. Jour. Anat.*, v. 26, 1919.

258. —— Problem of the Coracoid. *Anat. Rec.*, v. 19, 1920.

259. **Hart, P. C.** Entw. d. Schultergürtels der Schildkröten. *Tijdschr. Niederl. Dierk. Ver.*, v. 19, 1925.

260. **Haswell, W. A.** Elasmobranch Skeleton. *Proc. Linn. Soc. N.S.W.*, v. 9, 1884.

261. **Hoffmann, C. K.** Vergl. Anat. der Wirbeltiere : Schultergürtel u. Brustbein. *Niederl. Arch. Zool.*, v. 5, 1879.

262. **Hommes, J. H.** Devel. of Clavicula and Sternum in Birds and Mammals. *Tijdschr. Niederl. Dierk. Ver.*, v. 19, 1924.

263. **Howes, G. B.** Morph. of Mammalian Coracoid. *J. Anat. and Phys.*, v. 21, 1887.

264. —— Coracoid of Terrestrial Vertebrata. *P.Z.S.*, 1893.

265. **v. Huene, Fr.** Übersicht über der Reptilien der Trias. *Geol. u. Paläont. Abh.*, v. 6, 1902.

266. —— Praepubisfrage bei Dinosaurien u. anderen Reptilien. *Anat. Anz.*, v. 33, 1908.

267. —— Erythrosuchus (Pelycosimia). *Geol. Paläontol. Abh.*, v. 10, 1911.

268. **Huxley, T. H.** Animals intermediate between Reptiles and Birds. *Proc. Roy. Soc. London*, 1868.

269. —— Affinity between Dinosaurian Reptiles and Birds. *Quart. J. Geol. Soc. London*, v. 26, 1869.

270. **Johnson, A.** Devel. of Pelvic Girdle of Chick. *Quart. Jour. Micr. Sci.*, v. 23, 1883.

271. **Juhn, M.** Entw. d. Sternums bei Lacerta. *Acta Zool.*, v. 4, 1923.

272. **Knopfli, W.** Entw. des Brustschulterskeletts b. d. Vögeln. *Jena. Z. f. Naturw.*, 55, 1919 (Bibl.).

273. **Kravetz, L. P.** Entw. des Sternum- u. des Episternalapparats der Säugetiere. *Bull. Soc. Imp. Nat. Moscou*, v. 19, 1905 (1906).

274. **Lebedinsky, N. G.** Morph. u. Entw. des Vogelbeckens. *Jena. Zeitschr.*, v. 50, 1913.

275. —— Entw.-mech. Unters. an Amphibien : II. Die Umformungen des Grenzwirbels bei Triton, etc. *Biol. Zentralbl.*, v. 45, 1925.

276. **Levin, B.** Topogr. d. n. obturatorius in vorknorpeligen Vogelbecken. *Arb. Zool. Inst. Lettland. Univ.*, Riga, 1926.

277. **Lindsay, B.** Avian Sternum. *Proc. Zool. Soc. London*, 1885.

278. **Lydekker, R.** Coracoidal Element in Adult Sloths. *Proc. Zool. Soc.*, 1893.

279. **McGregor, J. H..** The Phytosauria. *Mem. Am. Mus. Nat. Hist.*, v. 9, 1906.

279a. —— Mesosaurus. *Comm. de Estudos d. Minas do Brazil*, 1908.

280. **Mehnert, E.** Entwickl. des os pelvis der Vögel. *Morph. Jahrb.*, v. 13, 1888.

281. —— Entwickl. des Beckengürtels bei Säugetieren. *Ibid.*, v. 15. 1889.

282. ——Entwickl. des Beckengürtels der Emys. *Ibid.*, v. 16, 1890.

283. **Merriam, J. C.** Triassic Ichthyosauria. *Mem. Univ. California*, v. 1, 1908.

284. **Meyer, H. v.** Ueber Belodon. *Palaeontogr.*, v. 10, 1863.

285. **Miner, R. W.** Pectoral Limb of Eryops, etc. *Bull. Am. Mus. N.H.*, v. 51, 1925.

286. **Nauck, E. Th.** Vergl. Morph. des Beutelknochens. *Morph. Jahrb.*, v. 55, 1925.

287. —— Entw. d. ventralen Schultergürtelabschnittes b. Alytes obstetricans. *Morph. Jahrb.*, v. 60, 1928.

287a. **Nauck, E. Th.** Episternum von Echidna. *Anat. Anz.*, v. 67, 1929.
288. **Parker, W. K.** Shoulder Girdle and Sternum in Vertebrata. *Ray Society*, 1868.
289. **Petronievics, B.**, and **Woodward, A. S.** Pectoral and Pelvic Arches of Archaeopteryx. *Proc. Zool. Soc. London*, 1917.
290. **Romer, A. S.** Comparison of Mammalian and Reptilian Coracoids. *Anat. Rec.*, v. 24, 1922.
291. —— Ilium in Dinosaurs and Birds. *Bull. Am. Mus. N.H.*, v. 46, 1922.
292. —— Locomotor Apparatus of Mammal-like Reptiles. *Ibid.*
293. —— Pelvic Musculature of Saurischian Dinosaurs. *Bull. Am. Mus. N.H.*, v. 48, 1923.
294. —— Pectoral Limb and Shoulder Girdle in Fish and Tetrapods. *Anat. Rec.*, 1924.
295. —— P. m. of Ornithischian Dinosaurs. *Acta Zool.*, v. 8, 1927.
296. **Schmalhausen, I.** Dermal Bones of Shoulder Girdle of Amphibia. *Rev. Zool. Russe*, v. 2, 1917.
297. **Seeley, H. G.** *Ornithosauria.* Cambridge, 1870.
297a. —— Mesosauria. *Quart. J. Geol. Soc.*, v. 48, 1892.
298. —— Nature of Shoulder Girdle in Sauropterygia. *Proc. Roy. Soc. London*, v. 51 and v. 54, 1892–93.
299. **Siebenrock, F.** Verbindungsweise des Schultergürtels mit den Schädel bei den Teleosteern. *Ann. K. K. Nat. Hofmuseums*, Wien, v. 16, 1901.
300. **Swinnerton, H. H.** Pectoral Skeleton of Teleosteans. *Quart. J. Micr. Sci.*, v. 49, 1905.
301. **Swirski, G.** Entw. des Schultergürtels u. d. Skel. d. Brustflosse des Hechtes. *Inaug. Diss.*, Dorpat, 1880.
302. **Vialleton, L** Ceinture pectorale et thorax des tétrapodes. Basin des tétrapodes. *Bull. Ac. Sc. Montpellier*, 1917.
303. **Villiers, C. G. S. de.** Brustschulterapp. b. d. Anuren. *Acta Zool.*, 3, 1922.
304. **Vogel, R.** Entw. d. Schultergürtels u. d. Brustflossenskelettes der Forelle. *Jena. Zeitschr. f. Naturw.*, v. 45, 1909.
305. **Wasnetzoff, W. W.** Function des Mesocoracoid. *Rev. Zool. Russe*, v. 3, 1922.
306. **Watson, D. M. S.** Batrachiderpeton lineatum. *Proc. Zool. Soc. London*, v. 2, 1913.
307. —— Evol. of Tetrapod Shoulder Girdle. *J. of Anat.*, v. 5, 1917.
308. —— Elasmosaurid Shoulder Girdle. *Proc. Zool. Soc. London*, 1924.
309. **Wiedersheim, R.** Becken der Fische. *Morph. Jahrb.*, v. 7, 1881.
310. —— Phylogenie der Beutelknochen. *Zeitschr. wiss. Zool.*, v. 53, 1892.
310a. —— Comp. Anatomy of Vertebrates, transl. by W. N. Parker, 3rd ed., 1907.
311. **Whipple, J. L.** Ypsiloid Apparatus of Urodeles. *Biol. Bull.*, v. 10, 1906.

CHAPTER V

Morphology of Head Region

312. **Addens, J. L.** Eye-muscle Nerves of Petromyzonts. *Proc. R. Acad. Sci. Amsterdam*, v. 31, 1928.
313. **Adelmann, H. B.** Devel. of Premandibular Head Cavities, etc. *J. of Morph. and Phys.*, v. 42, 1926.
314. —— Development of Eye-muscles of Chick. *J. Morph.*, v. 44, 1927.

315. **Ayers, H.** Unity of Gnathostome Type. *Am. Nat.*, v. 40, 1906.
316. —— Vertebrate Cephalogenesis : V. Origin of Jaw Apparatus and Trigeminus Complex, Amphioxus, etc. *J. Comp. Neur.*, v. 33, 1921.
317. **Balfour, F. M.** The Devel. of Elasmobranch Fishes. *Journ. Anat. and Phys.*, 1876–78.
318. —— *Comparative Embryology*, v. 2, London, 1881.
319. **Beccari, N.** Scheletro i miotomi di Trota, etc. *Arch. Ital. di Anat. ed Embriol.*, v. 19, 1922.
320. **Beer, G. R. de.** Segmentation of Head in Squalus. *Quart. Jour. Micr. Sci.*, v. 66, 1922.
321. —— Devel. of Head in Heterodontus. *Quart. J. Micr. Sci.*, v. 68, 1924.
322. —— Prootic Somites of Heterodontus and Amia. *Quart. J. Micr. Sci.*, v. 68, 1924.
323. —— Orbitotemporal Region of Skull. *Quart. Jour. Micr. Sci.*, v. 70, 1926,.
324. —— Devel. of Skull in Torpedo. *Ibid.*
325. **Born, G.** Über d. Nasenhöhlen u. d. Thränennasengang der Amphibien. *Morph. Jahrb.*, 2, 1876.
326. **Brock, G. T.** Devel. of Skull of Leptodeira. *Quart. Jour. Micr. Sci.*, v. 73, 1929.
327. **Brohmer, P.** Der Kopf e. Embryo v. Chlamydoselachus. *Jena Zeitschr.*, v. 44, 1909.
327a. **Broom, R.** Homology of Alisphenoid. *Rep. S. Afr. Assoc.*, 1907.
327b. —— Devel. of Marsupial Skull. *Proc. Linn. Soc. N.S. Wales*, v. 34, 1909.
328. **Burlet, H. M. de.** Entwickl. des Walsschädels (Balaenoptera). *Morph. Jahrb.*, v. 49, 1914, and v. 50, 1916.
329. **Chiarugi, G.** Dével. des nerfs vague, etc., chez les sauropsides et mammifères. Myotomes et nerfs, etc., des Amphibies anoures. *Arch. Ital. Biol.*, v. 13, 1890, and 15, 1891.
330. **Cords, E.** Nervensorgung d. Augenm. v. Petromyzon. *Anat. Anz.*, v. 66, 1928.
331. **Corning, H. K.** Entwickl. d. Kopf- und Extremitätenmuskulatur b. Reptilien. *Morph. Jahrb.*, v. 28, 1900.
332. —— Vergl. Anat. der Augenmuskulatur. *Morph. Jahrb.*, v. 29, 1900.
333. **Dohrn, A.** Stud. z. Urgeschichte d. Wirbeltierkörpers. Visceralbogen b. Petromyzon. *Mitt. Zool. Sta. Neapel*, v. 5, 1884. Zungenbein u. Kiefer d. Selachier. *Ibid.*, v. 6, 1885.
334. —— Mandibularhöhle der Selachier. Praemandibularhöhle. *Mitt. Zool. Sta. Neapel*, v. 17, 1904.
335. **Dücker, M.** Augen der Zyklostomen. *Jen. Zeitschr. f. Naturw.*, 60, 1924.
336. **Elliot, A. I. M.** Devel. of Frog. Part 1 : Segments of Occipital Region of Skull. *Quart. Jour. Micr. Sci.*, v. 51, 1907.
337. **Filatoff, D.** Metamerie der Kopfes v. Emys. *Morph. Jahrb.*, v. 37, 1907.
338. **Fraser, E. A.** Head-cavities and Devel. of Eye-muscles in Trichosurus. *Proc. Zool. Soc. London*, 1915.
339. **Froriep, A.** Occipitalen Urwirbel der Amnioten in Vergleich mit d. Selachier. *Verh. Anat. Ges.*, 1905.
340. **Fürbringer, M.** Über die Spino-occipitalen Nerven. *Festschr. v. C. Gegenbaur*, v. 3, Leipzig, 1897.
340a. **Fürbringer, P.** Muskulatur d. Kopfsk. d. Cyclostomen. *Jen. Zeitschr.*, v. 9, 1875.
341 **Gast, R.** Entwickl. des Oculomotorius, etc. *Mitt. Zool. Sta.*, v. 19, 1909.

342. **Gaupp, E.** Metamerie des Schädels. *Anat. Hefte Ergeb.*, v. 7, 1897 (Bibl.).

343. —— Entwicklung des Kopfskelettes. *Hertwigs Handb. Entw. Wirbeltiere*, vol. iii., Jena, 1905 (Bibl.).

344. **Gegenbaur, C.** Kopfnerven v. Hexanchus. *Jen. Zeitschr.*, v. 6, 1871.

345. —— Über d. Occipitalregion . . . der Fische. *Festschr. z. A. v. Kölliker*, Leipzig, 1887.

346. —— Metamerie des Kopfes. *Morph. Jahrb.*, v. 13, 1888.

347. **Goodrich, E. S.** Segmentation of Occipital Region in Urodela. *Proc. Zool. Soc. London*, 1911.

348. —— ' Proboscis Pores ' in Craniate Vertebrates. *Quart. Jour. Micr. Sci.*, v. 62, 1917.

349. —— Devel. of Segments of Head in Scyllium. *Quart. Jour. Micr. Sci.*, v. 63, 1918.

350. **Hatschek, B.** Studien ü. Entwickl. von Amphioxus. *Arb. Zool. Inst. Wien*, v. 4, 1881.

351. —— Mitth. ü. Amphioxus. *Zool. Anz.*, v. 7, 1884.

352. —— Metamerie des Amphioxus u. des Ammocoetes. *Verh. Anat. Ges. Wien*, 1892. Corrected *Anat. Anz.*, 8, 1893.

353. **Higgins, G. M.** Nasal Organs in Amphibia. *Illinois Biol. Monogr.*, v. 6, 1920 (Bibl.).

354. **Hoffmann, C. K.** Entw. der Selachii. *Morph. Jahrb.*, v. 27, 1899.

355. **Huxley, T. H.** On the Theory of the Vertebrate Skull. *Proc. Royal Soc.*, v. 9, 1857–59.

356. **Jackson, W. H.,** and **Clarke, W. B.** The Brain and Cranial Nerves of Echinorhinus spinosus, etc. *J. Anat. and Phys.*, v. 10, 1876.

357. **Jager, J.** Segmentierung der Hinterhauptregion. *Bez. der Cartilago Acrochordalis zur Mesodermcommissur*, Gröningen, 1924.

358. **Johnson, C. E.** Devel. of Prootic Somites, etc. (Chelydra). *Amer. J. Anat.*, v. 14, 1913.

359. **Johnston, J. B.** Morph. of Vertebrate Head. *Jour. Comp. Neurology*, v. 15, 1905.

360. **Kingsbury, B. F.,** and **Adelmann, H. B.** Morph. Plan of Head. *Quart. J. Micr. Sci.*, v. 68, 1924.

361. **Koltzoff, N. K.** Entwickl. d. Kopfes v. Petromyzon Planeri. *Anat. Anz.*, v. 16, 1899 ; *Bull. Soc. Imp. Nat. Moscou*, v. 15, 1901.

362. **Krawetz, L.** Entw. d. Knorpelschädels v. Ceratodus. *Bull. Soc. Nat. Moscou*, v. 24, 1911.

363. **Kupffer, C. von.** *Entwickl. des Kopfes von Ammocoetes.* München u. Leipzig, 1894.

363a. **Lamb, A. B.** Devel. of Eye-Muscles in Acanthias. *Am. J. Anat.*, v. 1, 1902.

364. **Levi, G.** Contrib. a. conosc. d. condrocranio cer. d. Mammiferi. *Monit. Z. Ital.*, Anno 20, 1909.

365. **Marshall, A. M.** On the Head Cavities, etc. *Q. Jour. Micr. Sci.*, v. 21, 1881.

366. —— Segmental Value of Cranial Nerves. *Jour. Anat. and Phys.*, v. 16, 1882.

367. **Matys, W.** Entwickl. der Muskulatur der Orbita b. Vögeln. *Arch. Anat. u. Phys.*, Anat. Abt. 1908.

368. **Neal, H. V.** Segmentation of Nervous Syst. in Squalus acanthias. *Bull. Mus. Comp. Zool. Harvard*, v. 31, 1898.

369. **Neal, H. V.** History of Eye Muscles. *J. of Morph.*, v. 30, 1918.
370. **Noordenbos, W.** Entw. des Chondrocraniums der Säugetiere. *Petrus Camper*, v. 3, 1905.
371. **Pedaschenko, D.** Entw. der Augenmuskelnerven. *Anat. Anz.*, v. 47, 1914.
372. **Pehrson, T.** Devel. of Teleostomian Fishes. *Acta Zool.*, v. 3, 1922.
373. **Platt, J. B.** Morph. of Vertebrate Head, based on a Study of Acanthias. *J. Morph.*, v. 5, 1891.
374. —— Devel. of Cartil. Skull in Necturus. *Morph. Jahrb.*, v. 25, 1897.
375. **Rex, H.** Entwickl. d. Augenmuskulatur der Ente. *Arch. mikr. Anat.*, v. 57, 1900.
376. **Rice, E. L.** Devel. of Skull in Skink, Eumeces. *J. of Morph.*, v. 34, 1920 (Bibl.).
377. **Rosenberg, E.** *Die Occipitalregion des Cranium . . . einiger Selachier*, Dorpat, 1884.
378. **Sagemehl, M.** Beitr. z. vergl. Anat. der Fische. I. Das Cranium von Amia calva. *Morph. Jahrb.*, v. 9, 1884. III. Das Cranium der Characiniden. *Ibid.*, v. 10, 1884. IV. Das Cranium der Cyprinoiden. *Ibid.*, v. 17, 1891.
379. **Salvi, G.** Cavités prémandibulaires . . . chez les Sauriens. *Bibl. Anat.*, v. 10, 1902.
380. **Scammon, R. E.** Devel. of Squalus. *Norm. Tafeln*, 1911.
381. **Schreiner, K. E.** Occipitalregion von Amia und Lepidosteus. *Zeitschr. f. wiss. Zool.*, vol. 72, 1902.
382. **Seters, W. H. van.** Dével. du chondrocrâne *d'Alytes obstetricans*. *Arch. de Biol.*, 32, 1922.
383. **Sewertzoff, A.** Entw. der Occipitalregion der niederen Vertebraten. *Bull. Soc. Imp. Nat. Moscou*, 1895.
384. **Sewertzoff, A. N.** Entwickl. des Selachierschädels. *Festschr. C. v. Kuppfer*, Jena, 1899.
385. **Sonies, F.** Entwickl. d. Chondrocraniums u. d. Knorp. Wirbelsäule b. d. Vögeln. *Petrus Camper*, v. 4, 1907.
386. **Stöhr, P.** Entw. d. Urodelenschädels. *Zeitschr. f. wiss. Zool.*, v. 33, 1879.
387. —— Entw. d. Anurenschädels. *Ibid.*, v. 36, 1881.
388. —— Entwickl. des Kopfskelettes der Teleostier. *Festschr. der J. Max, Univ. Würzburg*, v. 2, 1882.
389. **Swinnerton, H. H.** Morph. of Teleostean Head Skeleton (Gasterosteus aculeatus). *Quart. Jour. Micr. Sci.*, v. 45, 1902.
390. **Terry, R. J.** Primordial Cranium of Cat. *J. of Morph.*, v. 29, 1917.
391. **Toeplitz, Ch.** Bau u. Entwickl. der Knorpelschädels v. Didelphys. *Zoologica*, v. 27, 1920.
392. **Veit, O.** Besonderheiten am Primordialcranium v. Lepidosteus. *Anat. Hefte*, v. 33, 1907.
393. —— Entw. d. Primordialcranium von *Lepidosteus osseus*. *Anat. Hefte*, 1ste Abt. 44, 1911.
394. **Voit, M.** Primordialkranium des Kaninchens. *Anat. Hefte*, v. 38, 1909.
395. —— Abducensbrücke b. Menschen. *Anat. Anz.*, v. 52, 1919.
396. **Wijhe, J. W. van.** Mesodermsegmente d. Selachierkopfes. *Verh. K. Akad. Wet. Amsterdam*, v. 22, 1882 ; reprinted 1915.
397. —— Entwickl. des Kopf- und Rumpfskeletts von Acanthias. *Bijdr. t. d. Dierkunde*, v. 22, 1922.

398. **Wilson, J. T.**　Taenia clino-orbitalis in Echidna and Ornithorhynchus. *J. Anat. und Physiol.*, v. 40, 1906.

399. **Ziegler, H. E.**　Phylog. Entstehung des Kopfes. *Jen. Zeitschr. Naturw.*, v. 43, 1908.

CHAPTER VI

SKULL

400. **Adelmann, H. B.**　Prechordal Plate. *Am. J. Anat.*, v. 21, 1922.

401. **Allis, E. P.**　Petrosal Bone and Sphenoidal Region of Skull of *Amia calva*. *Zool. Bull.*, v. 1, 1897.

402. —— Cranial Muscles and Cranial and First Spinal Nerves in *Amia calva*. *J. Morph.*, v. 12, 1897.

403. —— Squamosal Intercalar Exoccipital Extrascapular Bones in *Amia calva*. *Anat. Anz.*, v. 16, 1899.

404. —— Skull and Cranial Muscles, etc., in Scomber. *J. Morph.*, v. 18, 1903.

405. —— Cranial Anat. of Mail-cheeked Fishes. *Zoologica*, v. 22, 1909.

406. —— Pituitary Fossa and Trigemino-facialis Chamber in Selachians. *Anat. Anz.*, v. 46, 1914.

407. —— in Ceratodus. *Ibid.*, v. 46, 1914.

408. —— Trigemino-facialis Chamber in Amphibians and Reptiles. *Ibid.*, v. 47, 1914.

409. —— Myodome, etc., in Fishes. *J. of Morph.*, v. 32, 1919.

410. —— Cranial Anatomy of Polypterus. *J. of Anat.*, v. 56, 1922.

410a. —— Myodome, etc., in Coelacanthidae, etc. *Ibid.*

411. —— Palatoquadrate in Coelacanthid Fishes. *Proc. Zool. Soc. London*, 1923.

412. —— Cranial Anatomy of Chlamydoselachus. *Acta Zool.*, v. 4, 1923.

413. —— Pituitary Fossa, Myodome, etc. *J. of Anat.*, v. 63, 1928 (Bibl.).

414. **Baur, G.**　Phylog. Arrangement of Sauropsida. *J. of Morph.*, v. 1, 1887.

415. —— Morph. of the Vertebrate Skull. *J. of Morph.*, v. 3, 1889.

416. —— Temporal Part of the Skull. *Am. Nat.*, v. 29, 1895.

417. —— Osteol. d. Schläfergegend d. höheren Wirbeltiere. *Anat. Anz.*, v. 10, 1895.

418. —— Morphologie des Unterkiefers der Reptilien. *Anat. Anz.*, 11, 1895.

419 —— The Stegocephali. *Anat. Anz.*, v. 11, 1896.

420. —— Systematische Stellung der Microsaurier. *Anat. Anz.*, v. 14, 1898.

421. **Beer, G. R. de.**　Studies on Vertebrate Head: Part 1: Fish. *Quart. J. Micr. Sci.*, v. 68, 1924. Part 2: Orbito-temporal region. *Ibid.*, v. 70, 1926.

421a. —— Devel. of Skull in Sturgeon, *Ibid.*, v. 69, 1925.

422. —— Early devel. of Chondrocranium of Salmo fario. *Quart. J. Micr. Sci.*, v. 71, 1927.

422a. —— Skull of Shrew. *Phil. Trans. R.S.*, v. 217, 1929.

423. **Bemmelen, J. F. van.**　Schädelbau der Monotremen. *Denkschr. Med. Nat. Ges. Jena*, v. 6, 1901.

424. **Boas, J. E. V.**　Schläfenüberdachung, etc. *Morph. Jahrb.*, v. 49, 1914.

425. **Böker, H.**　Schädel v. *Salmo salars*. *Anat. Hefte*, v. 49, 1913.

426. **Boulenger, G. A.**　Fishes (Teleostei). *Cambridge Nat. Hist.*, London, 1904.

426a. **Bradley, O. C.** Muscles, etc., of Skull in Lacertilia. *Zool. Jahrb.*, Abt. Anat., v. 18, 1903.

427. **Branson, E. B.** Structure and Relationships of American Labyrintho-dontidae. *J. of Geol.*, v. 13, 1905.

428. —— Skull of Pariotichus. *J. of Geol.*, v. 19, 1911.

429. **Bridge, T. W.** Cranial Osteology of Amia calva. *J. of Anat. and Phys.*, v. 11, 1877.

430. —— Osteology of Polyodon folium. *Phil. Trans. R.S.*, v. 169, 1879.

431. —— Cranial Anatomy of Polypterus. *Proc. Phil. Soc. Birmingham*, v. 6, 1887–89.

432. —— Skull of Osteoglossum formosum. *Proc. Zool. Soc.*, 1895.

433. —— Skull of Lepidosiren. *Trans. Zool. Soc.*, v. 14, 1897.

434. —— Fishes. *Cambridge Nat. Hist.*, v. 7, London, 1904.

435. **Broili, F.** Eryops megacephalus. *Palaeontogr.*, v. 46, 1899.

436. —— Pelycosaurierreste v. Texas. *Z. d. Deutsch. Geol. Ges.*, v. 56, 1904.

437. —— Stammreptilien. *Anat. Anz.*, v. 25, 1904.

438. —— Unpaare Elemente im Schädel von Tetrapoden. *Anat. Anz.*, v. 49, 1917.

439. **Broom, R.** Nasal-floor Bone in the Hairy Armadillo. *J. Anat. and Phys.*, v. 31, 1897.

440. —— Prevomer in Gomphognathus. *J. Anat. and Phys.*, v. 31, 1897.

441. —— Palate in Dicynodon. *Tr. S. Af. Phil. Soc.*, v. 11, 1901.

441a. —— Vomerine Bones. *Proc. Linn. Soc. N.S.W.*, 1904.

442. —— S. Afr. Pseudosuchian Euparkeria. *Ann. S. Afr. Mus.*, v. 3, 1906 ; *Proc. Zool. Soc. London*, 1913. Youngina. *Ibid.*, 1914.

443. —— Origin of Mammal-like Reptiles. *Proc. Zool. Soc. London*, 1908.

444. —— Permian Reptiles. *Bull. Am. Mus. Nat. Hist.*, v. 28, 1910.

445. —— Skull of Cynodonts. *Proc. Zool. Soc. London*, 1911.

446. —— Mesosuchus browni, etc. *Rec. Albany Mus.*, v. 2, 1913.

447. —— Squamosal in Mosasaurs and Lizards. *Ibid.*, v. 32, 1913.

448. —— Permian Temnospondylous Stegocephalians. *Ibid.*, v. 32, 1913.

449. —— Cotylosaurian, Pantylus. *Ibid.*, v. 32, 1913.

450. —— Structure of Mandible in Stegocephalia. *Anat. Anz.*, 45, 1913.

451. —— Origin of Mammals. *Phil. Trans. R.S.*, v. 206, B, 1914.

452. —— Diadectid Skull. *Bull. Am. Mus. Nat. Hist.*, v. 33, 1914.

453. —— S. Af. Dinocephalians and Am. Pelycosaurs. *Ibid.*, v. 33, 1914.

454. —— Permian Triassic and Jurassic Reptiles of S. Af. *Ibid.*, v. 25, 1915.

455. —— Persist. of Mesopterygoid in Reptilia. *Proc. Zool. Soc. London*, 1922.

456. —— Temporal Arches of Reptilia. *Ibid.*, 1922.

457. —— Skeleton of Youngina. *Ann. Transv. Mus.*, 1922.

458. —— Skull in Carnivorous Dinocephalian Reptiles. *Proc. Zool. Soc.*, 2, 1923.

459. —— Classification of Reptilia. *Bull. Am. Mus. Nat. Hist.*, v. 51, 1924.

460. —— Pareiasaurian Skull. *Proc. Zool. Soc. London*, 1924.

461. —— Origin of Lizards. *Proc. Zool. Soc.*, 1925.

462. —— Skeleton of Eosuchian (Palaeagama). *Ibid.*, 1926.

462a. —— Mammalian Presphenoid and Mesethmoid. *Ibid.*, 1926.

462b. —— Mammalian Basicranial Axis. *Ibid.*, 1927.

463. —— Sphenosuchus and Origin of Crocodiles. *Ibid.*, 1927.

464. —— Anningia. *Ibid.*, 1927.

465. **Bryant, W. L.** Structure of Eusthenopteron. *Bull. Buffalo Soc. Nat. Sci.*, v. 13, 1919.

465a. **Bulman, O. M.,** and **Whittard, W. F.** Branchiosaurus and Allied Genera. *Proc. Zool. Soc.*, 1926.

466. **Case, E. C.** Pariotichus incisivus. *Zool. Bull.*, v. 2, 1898–99.

467. —— Palaeontological Notes. *Contrib. fr. Walker Mus.*, Chicago, v. 1, 1902.

468. —— Osteology of Embolophorus. *Jour. Geol.*, 11, 1903.

469. —— Structure and Relationship of American Pelycosauria. *Am. Nat.*, 37, 1903.

470. —— Osteology of Diadectidae. *J. of Geol.*, v. 13, 1905.

471. —— Skull of Pelycosaurian Dimetrodon. *Trans. Am. Phil. Soc.*, v. 21, 1905.

472. —— Skull of Lysorophus. *Bull. Am. Mus. Nat. Hist.*, v. 24, 1908.

473. —— Revision of Cotylosauria. *Ibid.*, publ. 145, 1911 (Bibl.).

474. —— Amphibia and Pisces of Permian of N. Am. *Carnegie Inst.* publ. 146, 1911.

475. **Cole, F. J.** Cranial Nerves and Lateral Sense Organs of Fishes, genus Gadus. *Tr. Linn. Soc.*, s. 2, v. 7, 1896–1900.

476. **Collinge, W. E.** Lat. Canal System of Polypterus—of Lepidosteus. *Pr. Birmingham Phil. Soc.*, v. 8, 1891–93.

477. —— Morph. of Sensory Canal System in some Fossil Fishes. *Pr. Birmingham Phil. Soc.*, 9, 1895.

478. —— Sensory Canal System of Fishes, Teleostei, Suborder A, Physostomi. *Proc. Zool. Soc. London*, 1895.

479. **Cope, E. D.** Posterior Cranial Arches in Reptilia. *Trans. Am. Phil. Soc.*, v. 17, 1892.

480. —— Baur on the Temporal part of Skull, etc. *Am. Nat.*, v. 29, 1895.

481. —— Palaeozoic Order Cotylosauria. *Am. Nat.*, v. 30, 1896.

482. —— Reptilian Order Cotylosauria. *Proc. Am. Phil. Soc.*, v. 34, 1896.

483. **Cords, E.** Primordialcranium v. Perameles. *Anat. Hefte*, v. 52, 1915.

484. **Credner, H.** Stegocephalen und Saurier aus den Rothliegenden. *Zeit. der Deutsch. Geol. Ges.*, 1881–93.

485. —— Hylonomus and Petrobates and Discosaurus. *Zeit. d. Deut. Geol. Ges.*, v. 42, 1890.

486. **Dames, W.** Archaeopteryx. *Palaeont. Abh.*, v. 2, 1884.

487. **Daniel, J. F.** *Elasmobranch Fishes*, Berkeley, 1922; 2nd edit., 1928 (Bibl.).

488. **Fawcett, E.** Devel. of Human Sphenoid. *J. of Anat. and Physiol.*, v. 44, 1910.

489. —— Primordial Cranium of Microtus. *J. of Anat.*, v. 51, 1917.

490. —— P. C. of Erinaceus. *Ibid.*, v. 52, 1918.

491. —— P. C. of Poecilophoca. *Ibid.*, v. 52, 1918.

492. —— P. C. of Miniopterus. *Ibid.*, v. 53, 1919.

493. —— Septo-maxillare in Tatusia. *J. of Anat.*, v. 53, 1919.

494. **Fejérváry, G. J.** Dermal Bones of Skull. *Ann. Mus. Nat. Hungar.*, v. 16, 1918.

495. **Fischer, E.** Primordialcranium u. Talpa europaea. *Anat. Hefte*, v. 17, 1901.

496. —— Entwickl. der Affenschädels. *Z. Morph. u. Anthrop.*, v. 5, 1903.

497. **Fraas, E.** Labyrinthodonten d. swäb. Trias. *Palaeontogr.*, v. 36, 1889.

498. Froriep, A. Ganglion des Hypoglossus und Wirbelanlagen in der Occipitalregion. *Arch. f. Anat. u. Phys.*, 1882. Chorda Tympani. *Anat. Anz.*, v. 2, 1887.

499. —— Kraniovertebralgrenze b. d. Amphibien. *Arch. f. Anat. u. Phys.* Anat. Abt., 1917.

500. Frost, G. A. Int. Cranial Elements of Dapedius. *Q. J. Geol. Soc.*, v. 69, 1913.

501. Fuchs, H. Schläfengegend a. Schädel der Quadrupeden. *Anat. Anz.*, v. 35, 1909.

502. —— Septomaxillare e. rec. Säugetieres (Dasypus). *Ibid.*, v. 38, 1911.

503. —— Bau u. Entw. d. Schädels d. Chelone. Voeltzkow, *Reise in Ostafr.*, 1915.

504. Gaupp, E. Primordialcranium u. Kieferbogen v. Rana. *Morph. Arb.*, v. 2, 1893.

505. —— Schläfengegend am Knöch. Wirbelt.-Schädel. *Morph. Arb.*, v. 4, 1895.

506. —— Chondrocranium v. Lacerta. *Anat. Hefte*, v. 15, 1900.

507. —— Alte Probleme u. neure Arbeiten ü. d. Wirbeltierschädel. *Ergeb. Anat. u. Entw.*, v. 10, 1900 (Bibl.).

508. —— Über d. Ala temporalis des Säugerschädels u. d. Regio orbitalis. *Anat. Hefte*, v. 19, 1902.

509. —— Neue Deutungen a. d. Gebiete der Lehre vom Säugetierschädel. *Anat. Anz.*, v. 27, 1905.

510. —— Fragen a. d. Lehre von Kopfskelett. *Verh. Anat. Ges.*, 1906.

511. —— Morph. des Schädels von Echidna. *Denkschr. Med. Nat. Ges. Jena*, v. 6, 1907–8.

512. —— Ersten Wirbel u. d. Kopfgelenke v. Echidna. *Denkschr. Med. Nat. Ges. Jena*, v. 6, 1907.

513. —— Säugepterygoid u. Echidnapterygoid. *Anat. Hefte*, v. 42, 1910.

514. —— N. trochlearis der Urodelen. *Anat. Anz.*, v. 38, 1911.

515. —— Unterkiefer der Wirbeltiere. *Anat. Anz.*, v. 39, 1911.

516. Gegenbaur, C. Kopfskelet von Alepocephalus. *Morph. Jahrb.*, v. 4, suppl., 1878.

517. Goodrich, E. S. Classification of Reptilia. *Proc. Roy. Soc. London*, B, v. 89, 1916.

518. —— Head of Osteolepis. *J. Linn. Soc. London, Zool.*, v. 34, 1919.

519. —— Cranial Roofing-bones in Dipnoi. *J. Linn. Soc. London, Zool.*, v. 36, 1925.

520. —— Polypterus a Palaeoniscid? *Palaeobiologica*, v. 1, 1928.

521. Gregory, W. K. Orders of Mammalia. *Bull. Am. Mus. N.H.*, v. 27, 1910.

522. —— Critique . . . on Morph. of Vertebrate Skull. *J. of Morph.*, v. 24, 1913.

523. —— Origin of Tetrapoda. *Ann. N. York Ac. Sci.*, v. 26, 1915.

524. —— Lacrymal Bone. *Bull. Am. Mus. N.H.*, v. 42, 1920.

524a. Gregory, W. K., and **Noble, G. K.** Origin of Mammalian Alisphenoid. *J. Morph.*, v. 39, 1924.

525. Greil, A. Entw. d. Kopfes, etc., v. Ceratodus. *Denkschr. Med. Nat. Ges. Jena*, v. 4, 1913.

526. Hafferl, A. Neurocranium des Gecko. *Zeitschr. Anat. u. Entw.*, v. 62, 1921.

527. Heilmann, G. *Origin of Birds.* London, 1926.

528. **Howes, G. B.**, and **Swinnerton, H. H.** Devel. of Skeleton of Sphenodon. *Trans. Zool. Soc. London*, v. 16, 1901.
529. **Huene, F. v.** Os interparietale d. Mammalia. *Anat. Anz.*, v. 42, 1912.
530. —— Cotylosauria der Trias. *Palaeontogr.*, v. 59, 1912.
531. —— Skull Elements of Permian Tetrapoda. *Bull. Am. Mus. Nat. Hist.*, v. 32, 1913
531a. —— Lysorophus. *Anat. Anz.*, v. 43, 1913.
532. —— Osteol. d. Dicynodon-Schädels. *Palaeont. Zeitschr.*, v. 5, 1922.
533. **Huxley, T. H.** Fishes of Devonian, etc. *Mem. Geol. Surv.*, 1861. Crosso-pterygian Ganoids (Coelacanthini). *Ibid.*, 1866 and 1872.
533a. —— Classification of Birds. *Proc. Zool. Soc. London*, 1867.
534. —— Skull and Heart of Menobranchus. *Proc. Zool. Soc.*, 1874.
535. —— On Ceratodus Forsteri. *Proc. Zool. Soc.*, 1876.
536. **Jaekel, O.** Wirbeltierfunde a. d. Keuper Stegochelys (Triassochelys) dux. *Palaeont. Zeitschr.*, 2, 1918.
537. **Kindred, J. E.** Skull of Amiurus. *Illin. Biol. Monogr.*, v. 5, 1919.
538. —— Chondrocranium of Syngnathus fuscus. *J. Morph.*, v. 35, 1921. Devel. of Skull of Syngnathus. *Am. J. Anat.*, v. 33, 1924.
539. **Kingsley, J. S.** Bones of Reptilian Lower Jaw. *Am. Nat.*, v. 39, 1905.
540. **Kunkel, B. W.** Devel. of Skull of Emys. *J. of Morph.*, v. 23, 1912.
540a. **Lakjer, T.** Gaumenregion bei Sauriern. *Zool. Jahrb.*, Abt. Anat., v. 49, 1927.
541. **Lapage, E. O.** Septomaxillary. I. In Amphibia Urodela ; II. A. Anura and Reptilia. *J. Morph. and Phys.*, v. 45, 1928 ; and v. 46, 1928.
542. **Lehn, Ch.** Primordialschädels v. Polypterus. *Zeit. f. angew. Anat. u. Konstitut.*, v. 2, 1918.
543. **Lubosch, W.** Kiefergelenk der Edentaten u. Marsupialier. *Denkschr. Med. Nat. Ges. Jena*, v. 7, 1897–1912.
544. **Matthes, E.** Neuere Arbeiten ü. d. Primordialkranium der Säugetiere. *Ergeb. d. Anat. u. Entw.*, v. 23, 1921 (Bibl.).
545. **Mayrew, R. L.** Skull of Lepidosteus platostomus. *J. Morph.*, v. 38, 1924.
546. **Merriam, J. C.** Thalattosauria. *Mem. Calif. Ac. Sci.*, v. 5, 1905.
547. ——Triassic Ichthyosauria. *Mem. Univ. Calif.*, v. 1, 1908.
548. **Moodie, R. T.** Lateral Line System in Extinct Amphibia. *J. Morph.*, v. 19, 1908 ; and *J. Comp. Neurol.*, v. 25, 1916.
549. —— Coal Measure Amphibia of N. Am. *Carnegie Inst.* publ. 238, 1916.
550. —— Influence of Lat. Line Syst. on Osseous Elements. *J. Comp. Neurol.*, v. 34, 1922.
551. **Norman, J. R.** Devel. of Chondrocranium of Eel (Anguilla). *Phil. Trans.*, v. B, 214, 1926.
552. **Osawa, G.** Anat. der Hatteria. *Arch. f. mikr. Anat.*, v. 51, 1898.
553. **Osborn, H. F.** Occipital Condyles. *Am. Nat.*, v. 34, 1900.
554. —— Reptilian subclasses Diapsida and Synapsida. *Mem. Am. Mus. Nat. Hist.*, v. 1, 1903.
555. **Parker, T. J.** Cranial Osteology of Dinornithidae. *Tr. Zool. Soc.*, v. 25, 1895.

Parker, W. K.
Struct. and devel. of Skull of—
556. —— Ostrich. *Phil. Trans. R.S.*, v. 156, 1866.
557. —— Fowl. *Ibid.*, v. 159, 1869.
558. —— Rana. *Ibid.*, v. 161, 1871.

Parker, W. K.
Struct. and devel. of Skull of—
559. —— Batrachia. *Ibid.*, v. 161, 1871.
560. —— Salmon. *Ibid.*, v. 163, 1873.
561. —— Pig. *Ibid.*, v. 164, 1874.
562. —— Urodela. *Ibid.*, v. 167, 1876.
563. —— Tropidonotus. *Ibid.*, v. 169, 1879.
564. —— Lacertilia. *Ibid.*, v. 170, 1880.
565. —— Acipenser. *Ibid.*, v. 173, 1882.
566. —— Lepidosteus. *Ibid.*, v. 173, 1882.
567. —— Edentata and Insectivora. *Ibid.*, v. 176, 1885.
568. —— Birds. *Trans. Zool. Soc.*, v. 9 and 10, 1875–76.
569. —— Sharks and Skates. *Ibid.*, v. 10, 1879.
570. —— Crocodilia. *Ibid.*, v. 11, 1883.
571. —— Opisthocomus. *Ibid.*, v. 13, 1891.
572. —— Birds. *Tr. Linn. Soc. Zool.*, v. 1, 1875.
573. —— Urodela. *Ibid.*, v. 2, 1879–88.
574. —— Devel. of Green Turtle (Chelone viridis). *'Challenger' Reports*, v. 1, 1880.
575. **Pollard, H. B.** Anat. and Phylog. Position of Polypterus. *Zool. Jahrb.* Abt. Anat., v. 5, 1892.
576. **Pycraft, W. P.** Palaeognathae and Neognathae. *Tr. Zool. Soc.*, v. 15, 1900.
577. **Regan, C. T.** Skeleton of Lepidosteus. *Proc. Zool. Soc. London*, 1923.
578. **Ridewood, W. G.** Cranial Osteology of Elopidae and Albulidae, etc. *Proc. Zool. Soc.*, v. 2, 1904.
579. —— Cranial Osteology of Clupeoid Fishes. *Proc. Zool. Soc.*, v. 2, 1904.
580. —— Cranial Osteol. of Osteoglossidae, Pantodontidae and Phractolaemidae. *Jour. Linnean Soc.*, v. 29, 1904.
581. —— Cranial Osteol. of Mormyridae, Notopterydae, and Hyodontidae. *Jour. Linnean. Soc.*, v. 29, 1905.
582. **Riese, H.** Anatomie des Tylototriton verrucosus. *Zool. Jahrb.* Abt. Anat., v. 5, 1891.
583. **Schauinsland, H.** Entw. u. Anat. der Wirbeltiere: Sphenodon, Chamäleo, Callorhynchus. *Zoologica*, 16, 1903.
584. **Schleip, W.** Entw. der Kopfknochen b. d. Lachs u. d. Forelle. *Anat. Hefte*, v. 23, 1904.
Seeley, H. G.
Structure, etc., of Fossil Reptilia—
585. —— Protorosaurus. *Phil. Trans. R.S.*, v. 178, B, 1887.
586. —— Pareiasaurus. *Ibid.*, v. 179, B, 1888.
587. —— Keirognathus. *Ibid.*
588. —— Anomodont Reptilia. *Ibid.*, v. 180, B, 1889.
589. —— Diademodon. *Ibid.*, v. 185, B, 1894.
590. —— Gomphodontia. *Ibid.*, v. 186, B, 1895.
591. —— Cynodontia. *Ibid.*, v.
592. **Sewertzoff, A. N.** Entwickl. des *Ceratodus Forsteri*. *Anat. Anz.*, v. 21, 1902.
593. —— Morph. d Schädels v. *Polypterus delhesi*. *Anat. Anz.*, v. 59, 1925.
594. —— Head Skeleton and Muscles of Acipenser ruthenus. *Acta Zoologica*, v. 9, 1928.
595. **Seydel, O.** Nasenhöhle u. Mundhöhlendache von Echidna u. das Gaumen

der Wirbeltiere. *Denk. Med. Nat. Ges. Jena*, v. 3, Zool. Forsch., 1899 (Bibl.).

596. **Shaner, R. F.** Devel. of Skull of Turtle. *Anat. Rec.*, v. 32, 1925.

597. **Shiino, K.** Chondrocranium v. Crocodilus. *Anat. Hefte*, v. 50, 1914.

598. **Siebenrock, F.** Osteologie d. Hatteria-kopfes. *Sitz. Ak. Wiss. Wien,* v. 102, 1893.

599. —— Skelet d. Lacerta. *Ibid.*, v. 103, 1894.

600. —— Skelet d. Agamidae. *Ibid.*, v. 104, 1895.

601. —— Kopfskelet der Schildkroten. *Ibid.*, v. 106, 1897.

602. **Sollas, J. B. J.**, and **Sollas, W. J.** Skull of Dicynodon. *Phil. Trans. R.S.*, v. 204, B, 1913.

603. **Sollas, W. J.** Lysorophus. *Phil. Trans. R.S.*, v. 209, 1920.

604. **Stadtmüller, F.** Entw. d. Kopfskeletts d. Salamandra. *Zeit. f. Anat. u. Entw.*, v. 75, 1924.

605. **Stensiö, E. A. S.** Coelacanthiolen a. d. Oberdevon. *Palaeont. Zeitschr.*, v. 4, 1922.

606. —— Notes on Crossopterygiańs. *Proc. Zool. Soc.*, 1922.

607. —— Downtonian and Devonian Vert. of Spitzbergen : Cephalaspidae. *Akad. Oslo*, 1927.

608. **Sushkin, P. P.** Schädel v. Tinunculus. *Nouv. Mém. Soc. Imp. Nat. Moscou*, v. 16, 1899.

608a. —— Cranial Morph. of Captorhinus. *Palaeobiologica*, v. 1, 1928.

609. **Sutton, J. B.** Parasphenoid, Vomer, and Palatopterygoid Arcade. *Pr. Zool. Soc.*, 1884.

610. **Thévenin, A.** Anciens quadrupèdes de France. *Ann. de. Paléont.*, v. 5, 1910 (Bibl.).

611. **Thyng, F. W.** Squamosal Bone in Tetrapodous Vertebrata. *Proc. Bost. Soc. N.H.*, v. 32, 1906 (Bibl.).

612. **Tonkoff, W.** Entwickl. des Hühnerschädels. *Anat. Anz.*, v. 18, 1900.

613. **Traquair, R. H.** Cranial Osteology of Polypterus. *Jour. Anat. and Phys.*, v. 5, 1871.

614. —— Struct., etc., of Cheirolepis. *Ann. Mag. Nat. Hist.*, v. 15, 1875.

615. —— Structure of Lower Jaw in Rhizodopsis and Rhizodus. *Ann. Mag. Nat. Hist.*, v. 19, 1877.

616. —— Palaeoniscidae. *Monogr. Palaeontogr. Soc.*, 1877.

617. —— Genera Dipterus, Palaedaphus, Holodus and Cheirodus. *Ann. Mag. Nat. Hist.*, v. 2, 1878.

618. —— Struct. and Affinities of Platysomidae. *Trans. Roy. Soc. Edinburgh*, v. 29, 1879.

619. —— Cranial Osteology of Rhizodopsis *Trans. Roy. Soc. Edinburgh*, v. 30, 1883.

620. —— Chondrosteus acipenseroides. *Geol. Mag.*, v. 4, 1887.

621. —— Struct. and Classif. of Asterolepida. *Ann. Mag. Nat. Hist.*, v. 2, 1888.

622. —— Fossil Dipnoi and Ganoids of Fife and Lothians. *Proc. Roy. Soc. Edinburgh*, v. 17, 1890.

623. **Versluys, J.** Parasphenoid bei Dermochelys. *Zool. Jahrb.*, v. 28, 1909.

624. —— Streptostylie bei Dinosaurien. *Ibid.*, v. 30, 1910.

625. —— Das Streptostylie-Problem. *Ibid.*, suppl. 15, v. 2, 1912.

626. —— Phylogenie der Schläfengruben u. Jochbogen. *Sitz. Heidelb. Ak. Wiss*, 1919.

627. —— Schädel d. Trachodon. *Abh. Senckenb. Nat. Ges.*, v. 38, 1923.

628. **Vrolik, A. J.** Verknöcherung d. Schläfenbeins der Säugetiere. *Niederl. Arch. f. Zool.*, v. 1, 1873.

629. —— Studien ü. d. Verknöcherung . . . der Teleostier. *Niederl. Arch. f. Zool.*, v. 1, 1873.

630. **Walther, J.** Entw. d. Deckknochen des Hechtes. *Jen. Zeitschr.*, v. 16, 1883.

631. **Watson, D. M. S.** Larger Coal Measure Amphibia. *Mem. Manchester Lit. Phil. Soc.*, v. 57, 1912.

631a. —— Skull of Diademodon. *Ann. Mag. Nat. Hist.*, v. 8, 1911.

632. —— Reptilian Lower Jaws. *Ibid.*, v. 10, 1912.

633. —— Micropholis stowi. *Geol. Mag.*, v. 10, 1913.

634. —— Skull, Brain, etc., of Diademodon. *Ibid.*, v. 12, 1913.

635. —— Anomodont Brain-case. *Anat. Anz.*, v. 44, 1913.

636. —— Varanosaurus. *Ann. Mag. Nat. Hist.*, v. 13, 1914.

637. —— Skull of Pareiasaurian. *Proc. Zool. Soc. London*, 1914.

638. —— Pleurosaurus and Lizard's Skull. *Ann. Mag. Nat. Hist.*, v. 14, 1914.

639. —— Procolophon. *Proc. Zool. Soc. London*, 1914.

640. —— Deinocephalia. *Ibid.*, 1914. Cynodontia. *Ibid.*, 1920.

641. —— Carnivorous Therapsids. *Ibid.*, 1914.

642. —— Monotreme Skull. *Phil. Trans. R.S.*, v. 207, 1916.

643. —— Seymouria. *Proc. Zool. Soc. London*, 1919.

644. —— Evol. and Origin of Amphibia. 1. *Phil. Trans. Roy. Soc.*, v. 209, B, 1919 ; 2. *Ibid.*, v. 214, B, 1925 (Bibl.).

645. —— On Coelacanth Fish. *Ann. Mag. N.H.*, v. 8, 1921.

646. —— Structure of Palaeoniscids. *Proc. Zool. Soc. London*, 1925.

647. **Watson, D. M. S., and Day, H.** Notes on Palaeozoic Fishes. *Mem. Manchester Lit. Phil. Soc.*, 1916.

648. **Watson, D. M. S., and Gill, E. L.** Structure of Palaeozoic Dipnoi. *J. Linn. Soc. Zool.*, v. 35, 1923.

649. **Wellburn, E.** Genus Coelacanthus, etc. *Proc. Yorks. Geol. and Pal. Soc.*, v. 14, 1902.

650. **Wells, Grace A.** Skull of Acanthias vulgaris. *J. of Morph.*, v. 28, 1917.

651. **Wiedersheim, R.** Kopfskelet der Urodelen. *Morph. Jahrb.*, v. 3, 1877.

652. —— *Anat. der Gymnophionen.* Jena, 1879.

653. —— Skelet, etc., v. Lepidosiren annectens. *Morph. Studien*, 1, Jena, 1880.

654. **Wijhe, J. W. v.** Visceralskelet u. Nerven des Kopfes der Ganoiden u. von Ceratodus. *Niederl. Arch. f. Zool.*, v. 5, 1879–82.

655. **Williston, S. W.** Temporal Arches of Reptilia. *Biol. Bull.*, v. 7, 1904.

656. —— Lysorophus a Permian Urodele. *Biol. Bull.*, v. 15, 1908.

657. —— Permian Vertebrates : Trematops. *J. of Geol.*, v. 17, 1909.

658. —— Cacops, Desmospondylus. *Bull. Geol. Soc. Am.*, v. 21, 1910.

659. —— Mandible in Amphibians and Reptiles. *J. of Geol.*, v. 21, 1913.

660. —— Trimerorhachis. *J. of Geol.*, v. 23, 1915.

661. —— Synopsis of Am. Permocarboniferous Tetrapoda. *Contrib. Walker Mus.*, v. 1, 1916.

662. **Winslow, C. M.** Chondrocranium in Ichthyopsida. *Tufts Coll. Studies*, No. 5, 1898.

663. **Woodward, A. Smith.** *Catalogue of Fossil Fishes in Brit. Mus.* 4 vols. London, 1889–1901.

664. **Woodward, A. Smith.** Cranial Osteology of . . . Lepidotus and Dapedius. *Proc. Zool. Soc.*, 1893.

665. —— Fossil Fishes of English Chalk. *Palaeontogr. Society*, London, 1902.

666. **Zimmermann, S.** Chondrocr. v. *Angius fragilis*. *Anat. Anz.*, v. 44, 1913.

CHAPTER VII

VISCERAL ARCHES AND LABIAL CARTILAGES

667. **Allis, E. P.** Hyomandibular of Gnathostome Fish. *J. of Morph.*, v. 26, 1915.

668. —— Labial Cartilages of Raja. *Quart. Jour. Micr. Sci.*, v. 62, 1917.

669. —— Origin of Hyomandibular. *Anat. Rec.*, v. 15, 1918.

670. —— Polar and Trabecular Cartilages. *J. of Anat.*, v. 57, 1922 ; v. 58, 1923 ; and v. 59, 1925.

671. —— Hyomandibula and Preoperculum. *Ibid.*, v. 62, 1928.

672. **Berrill, N. J.** Devel. of Skull of Sole and Plaice. *Quart. Jour. Micr. Sci.*, v. 69, 1925.

673. **Braus, H.** Kiemenapparat von *Heptanchus*. *Anat. Anz.*, v. 29, 1906.

674. **Daniel, J. F.** Anat. of Heterodontus : II. Endoskeleton. *J. Morph.*, v. 26, 1915.

675. **Drüner, L.** Zungenbein, Kiemenbogen- u. Kehlkopfmuskeln der Urodelen. 1 Th., *Zool. Jahrb.*, Abt. Anat., v. 15, 1902; 2 Th., *Zool. Jahrb.*, Abt. Anat., v. 19, 1904.

676. **Edgeworth, F. H.** Quadrate in Cryptobranchus, Menopoma, and Hynobius. *J. of Anat.*, v. 57, 1923.

677. —— Larval Hyobranchial Skeleton and Musculature of Cryptobranchus, etc. *Ibid.*, v. 57, 1923.

678. —— Autostylism of Dipnoi and Amphibia. *J. of Anat.*, v. 59, 1925.

679. —— Hyomandibula of Selachii, Teleostomi, and Ceratodus. *Ibid.*, v. 60, 1926.

680. **Foote, E.** Extra-branchial Cartilages. *Anat. Anz.*, v. 13, 1897.

681. **Fürbringer, K.** Beitr. z. K. d. Visceralskeletts d. Selachier. *Morph. Jahrb.*, v. 31, 1903.

682. —— Morph. d. Skeletes der Dipnoer, etc. *Denk. Med. Nat. Ges. Jena*, v. 4, 1904.

683. **Gaupp, E.** Das Hyobranchialskelet. *Anat. Hefte, Ergeb.*, v. 14, 1904.

684. **Gibian, A.** Hyobranchialskelett der Haie. *Morph. Jahrb.*, v. 45, 1913 (Bibl.).

685. **Goodey, T.** Skel. Anat. of Chlamydoselachus. *Proc. Zool. Soc. London*, 1910.

686. **Göppert, E.** Kehlkopf der Amphibien u. Reptilien. *Morph. Jahrb.*, v. 26, 1898 ; v. 28, 1899.

687. —— Vergl. Anat. des Kehlkopfes. *Denkschr. Med. Nat. Ges. Jena*, v. 6, 1901 ; v. 11, 1904 (Bibl.).

688. **Gregory, W. K.** Relations of Anterior Visceral Arches to Chondrocranium. *Biol. Bull.*, v. 7, 1904.

689. **Hawkes, O. A. M.** Vestigial Sixth Branch. Arch in Heterodontidae. *J. Anat. and Phys.*, v. 40, 1905.

690. **Jaekel, O.** Das Mundskelett der Wirbeltiere. *Morph. Jahrb.*, v. 55, 1925.

691. **Kallius, E.** Entwickl. des Kehlkopfes. *Anat. Hefte*, v. 9, 1897.

692. **Kesteven, H. L.** Palate and Upper Jaw of Fishes. *J. of Anat.*, v. 56, 1922.

693. **Kravetz.** Entw. d. Knorpelschädels v. Ceratodus. *Bull. Soc. Nat. Moscou*, 1911.

694. **Krivetski, A.** Morph. de l'arc hyoide chez les Sélaciens. *Rev. Zool. Russe*, v. 2, 1917.

695. **Luther, A.** N. trigeminus innervierte Muskulatur der Selachier. *Acta Soc. Sc. Fennicae*, v. 36-7, 1909. Ganoiden u. Dipneusten. *Ibid.*, v. 41, 1913.

696. **Pollard, H. B.** Oral Cirri of Siluroids. *Zool. Jahrb.*, Abt. Morph., v. 8, 1895.

697. —— Suspension of Jaws in Fish. *Anat. Anz.*, v. 10, 1895.

698. **Ridewood, W. G.** Hyoid Arch of Ceratodus. *Proc. Zool. Soc.*, 1894.

699. **Schmalhausen, J. J.** Suspensorialapparat d. Fische. *Anat. Anz.*, v. 56, 1923.

700. —— Autostylie d. Dipnoi. *Ibid.*

701. **Sewertzoff, A. N.** Évolution des Vertébrés: Cyclostomes, etc. *Arch. russes d'Anat., d'Hist. et d'Embr.*, v. 1, 1916.

701a. —— Appareil viscéral des Elasmobranches. *Publ. Staz. Zool. Napoli*, v. 18, 1927.

702. **White, P. J.** Skull and Visceral Skeleton of Laemargus. *Tr. R.S. Edin.*, v. 37, 1891–95.

703. **Woodward, A. S.** Mandib. and Hyoid Arches in Hybodus. *Proc. Zool. Soc. London*, 1886.

CHAPTER VIII

MIDDLE EAR AND EAR OSSICLES

704. **Baur, G.** Quadrate of Mammalia. *Quart. J. Micr. Sci.*, v. 28, 1887; *Biol. Centralbl.*, v. 6.

705. **Bender, O.** Homologie des Spritzloches der Selachier u. d. Paukenhöhlen, etc. *Anat. Anz. Ergh.*, v. 30, 1907.

706. —— Entwickl. d. Visceralsk. bei Testudo. *Abh. bayer. Akad. Wiss., Math.-phys. Kl.*, v. 25, 1912.

707. **Bondy, G.** Vergl. Anat. d. Gehörorgans d. Säuger. *Anat. Hefte*, 1 Abt., v. 35, 1907.

708. **Broman, I.** Die Entwickl. der Gehörknöchelchen, p. 507. *Anat. Hefte* 1 Abt., v. 11, 1899.

709. **Broom, R.** Theriodont Mandible, etc. *Proc. Zool. Soc. London*, 1904.

710. —— Internal Ear in Dicynodon and Homology of Auditory Ossicles. *Ibid.*, 1912.

711. **Cope, E. D.** Hyoid and Otic Elements in Batrachia. *J. Morph.*, v. 2, 1889.

712. **Cords, E.** Entwickl. d. Paukenhöhle v. Lacerta. *Anat. Hefte*, Abt. 1, v. 52, 1915.

713. **Dollo, J.** Malleus of Lacertilia. *Quart. J. Micr. Sci.*, v. 23, 1883.

714. **Doran, A. H. G.** Morph. of Mammalian Ossicula auditus. *Trans. Linn. Soc. Zool.*, v. 1, 1878.

715. **Dreyfuss, R.** Entw. des Mittelohres u. d. Trommelfels. *Morph. Arb.*, v. 2, 1893.

716. Drüner, L. Anat. u. Entw. des Mittelohres beim Menschen u. bei der Maus. *Anat. Anz.*, v. 24, 1904.

717. Dunn, E. R. Sound-transmitting App. of Salamanders and Phylog. of Caudata. *Am. Nat.*, v. 56, 1922.

718. Edgeworth, F. H. Devel. of Mandibular and Hyoid Muscles. *Quart. J. Micr. Sci.*, v. 59, 1914.

719. Emmel, V. E. Relation of Chorda Tympani in Microtus. *J. Comp. Neur.*, v. 14, 1904.

720. Eschweiler, R. Entw. d. schalleit. Apparates. *Arch. mikr. Anat. u. Entw.*, v. 63, 1904.

721. —— Entw. d. M. stapedius u. d. Stapes. *Ibid.*, v. 77, 1911.

722. Esdaile, Ph. C. Struct. and Devel. of Skull of Perameles. *Phil. Trans. Roy. Soc.*, B, v. 207, 1916.

723. Fox, H. Devel. of Tympano-Eustachian Passage, etc. *Proc. Acad. Nat. Sci. Philad.*, v. 53, 1901.

724. Frey, H. Hammer-Amboss Verbindung der Säuger. *Anat. Hefte*, v. 44, 1911.

725. Froriep, A. Homologon der Chorda tympani bei niederen Wirbelthieren. *Anat. Anz.*, v. 2, 1887.

726. —— Anlagen v. Sinnesorganen am Facialis. *Arch. Anat. u. Phys.*, Abt. Anat., 1885.

727. Fuchs, Hugo. Entw. des Operculums der Urodelen u. d. Distelidiums (' Columella ' auris) einiger Reptilien. *Anat. Anz. Ergh.*, v. 30, 1907.

728. Fuchs, H. Über Knorpelbildung in Decknochen u. Unters. u. Betr. ü. Gehörknöchelchen. *Arch. Anat. Phys.*, Abt. Anat., Suppl., 1909.

729. Gadow, H. Evolution of Auditory Ossicles. *Anat. Anz.*, 19, 1901.

730. —— Modifications of Visceral Arches. *Phil. Trans. R.S.*, v. 186, 1895.

731. Gaupp, E. Ontog. u. Phylog. des schalleitenden Apparates. *Ergeb. Anat. u. Entw.*, v. 8, 1899 (Bibl.).

732. —— Die Reichertsche Theorie. *Arch. Anat. u. Physiol.*, Abt. Anat., Suppl. v., 1913 (Bibl.).

733. Goldby, F. Devel. of Columella auris in Crocodilia. *J. Anat.*, v. 59, 1925.

734. Goodrich, E. S. Chorda tympani and Middle Ear in Reptiles. *Quart. J. Micr. Sci.*, v. 61, 1915.

735. Gregory, W. K. Orders of Mammals. *Bull. Am. Mus. Nat. Hist.*, v. 27, 1910.

736. Hammar, J. A. Entw. des Vorderdarms, 1 Abt. Morph. d. Schlundspalten —Mittelohrraumes, etc. *Arch. mikr. Anat.*, v. 59, 1902.

737. Hoffmann, C. K. Ontw. v. h. Gehoororgaan b. de Reptilien. *Natuurk. Verh. Kon. Ac. Amsterdam*, v. 28, 1889.

738. Huxley, T. H. Devel. of Columella auris in Amphibia. *Nature*, v. 11, 1875.

739. —— Malleus and Incus of Mammalia. *Proc. Zool. Soc. London*, 1869.

740. Jenkinson, J. W. Devel. of Ear-bones in Mouse. *J. Anat. and Phys.*, v. 45, 1911.

741. Kampen, P. N. van. Tympanalgegend des Säugetierschädels. *Morph. Jahrb.*, v. 34, 1905.

742. Killian, G. Anat. u. Entw. d. Ohrmuskeln. *Anat. Anz.*, v. 5, 1890.

743. Kingsbury, B. F. Columella auris and Nervus facialis in Urodela. *J. Comp. Neur.*, v. 13, 1903.

744. Kingsbury, B. F., and Reed, H. D. Columella auris in Amphibia. *Anat. Rec.*, v. 2, 1908 ; *J. of Morph.*, v. 20, 1909.

745. **Kingsley, J. S.** Ossicula auditus. *Tuft's Call. Studies,* 1900.

746. **Kingsley, J. S.,** and **Ruddick, W. H.** Ossicula auditus and Mammalian Ancestry. *Am. Nat.,* 33, 1899.

747. **Klaauw, C. J. van d.** Entw. des Entotympanicus. *Tydschr. Nederl. dierk. Ver.,* v. 18, 1922.

748. —— Skelettstückchen i. d. Sehne d. Musculus stapedius. *Zeitschr. Anat. u. Entw.,* v. 69, 1923.

748a. —— Skelettst. von Paauw u. d. Verlauf d. Chorda tympani. *Anat. Anz.,* v. 57, 1923.

748b. —— Bau u. Entw. der Gehörknöchelchen. *Ergeb. d. Anat. Entw.,* v. 25, 1924 (Bibl.).

749. **Krause, G.** Die Columella der Vögel. Berlin, 1901.

750. **Litzelmann, E.** Visceralapparat der Amphibien. *Zeitsch. f. Anat. u. Entw.,* v. 67, 1923.

751. **Magnien, L.** Anat. comp. de la corde du tympan des oiseaux. *C.R. Acad. Sc. Paris,* v. 101, 1885.

752. **Marcus, H.** Gymnophionen : Entwickl. des Kopfes. *Morph. Jahrb.,* v. 40, 1910.

753. **Möller, W.** Entwickl. d. Gehörknöchelchens b. d. Kreuzotter. *Arch. mikr. Anat.,* v. 65, 1905.

754. **Noack.** Entwickl. d. Mittelohres v. Emys. *Arch. mikr. Anat.,* v. 69, 1907.

755. **Okajima, K.** Entwickl. d. Gehörknöchelchens b. d. Schlangen. *Anat. Hefte,* v. 53, 1915.

756. **Osawa, G.** Anat. d. Hatteria. *Arch. mikr. Anat.,* v. 51, 1898.

757. **Palmer, W. R.** Lower Jaw and Ear Ossicles of Foetal Perameles. *Anat. Anz.,* v. 43, 1913.

758. **Peter, K.** Entwickl. des Schädels von *Ichthyophis glutinosus. Morph. Jahrb.,* v. 25, 1896–98.

759. **Peyer, B.** Entwickl. d. Schädelskeletts v. Vipera. *Morph. Jahrb.,* v. 44, 1912.

760. **Reed, H. D.** Sound-transmitting Apparatus in Necturus. *Anat. Rec.,* v. 9, 1915.

761. —— Morph. of Sound-transmitting Apparatus in Caudate Amphibia, etc. *J. of Morph.,* v. 33, 1920.

762. **Salensky, W.** Entwickl. der knorpeligen Gehörknöchelchen bei Säugetieren. *Morph. Jahrb.,* 6, 1880.

763. **Sarasin, P.** and **F.** Entwickl. u. Anat. d. Ichthyophis. *Ergeb. Nat. Forsch. Ceylon,* v. 2, 1890.

764. **Shiino, K.** Chondrocranium v. Crocodilus. *Anat. Hefte,* v. 50, 1914.

765. **Smith, G. W.** Middle Ear and Columella of Birds. *Quart. J. Micr. Sci.,* v. 48, 1905.

766. **Smith, L. W.** Columella auris in Chrysemis. *Anat. Anz.,* v. 46, 1914.

767. **Spemann, H.** Entw. d. Tuba Eustachii u. d. Kopfskeletts v. *Rana temporaria. Zool. Jahrb.,* Abt. Anat., v. 11, 1898.

768. **Sushkin, P.** Mandibular and Hyoid Arches in early Tetrapoda. *Paläont. Zeitschr.,* v. 8, 1927.

769. **Versluys, J.** Mittl. u. äussere Ohrsphäre d. Lacertilia u. Rhynchocephalia. *Zool. Jahrb.,* Abt. Anat. u. Entw., v. 12, 1898.

770. —— Entwickl. der Columella auris b. d. Lacertilien. *Zool. Jahrb.,* Abt. Anat. u. Ont., v. 19, 1903.

771. **Villy, F.** Devel. of Ear and Accessory Organs in Common Frog. *Quart. J. Micr. Sci.,* v. 30, 1890.

772. **Witebsky, M.** Entwickl. d. schalleit. Apparates d. Axolotl. *Inaug. Diss. Berlin,* 1896.

773. **Wyeth, F. J.** Devel. of Audit. Apparatus in Sphenodon. *Phil. Trans. Roy. Soc.,* B, 212, 1924.

CHAPTER IX

VISCERAL CLEFTS AND GILLS

774. **Assheton, R.** The Devel. of Gymnarchus niloticus. *Budgett Mem. Vol.,* London, 1907.

775. **Biétrix, E.** *Morph. du système circulatoire . . . des poissons.* Paris, 1895.

776. **Budgett, J. S.** Breeding Habits of some West African Fishes, etc. *Trans. Zool. Soc.,* v. 16, 1901.

777. **Clemens, P.** Äusseren Kiemen der Wirbeltiere. *Anat. Hefte,* v. 5, 1894.

778. **Dean, B.** Embryology of Bdellostoma. *Festschr. f. C. v. Kupffer,* 1899.

779. —— Notes on Japanese Myxinoids. *J. Coll. Sci. Tokyo,* v. 19, 1904.

780. **Dohrn, A.** Spritzlochkieme der Selachier, etc. *Mitth. Zool. Sta. Neapel,* v. 7, 1886.

781. **Faussek, V.** Histologie der Kiemen bei Fischen u. Amphibien. *Arch. mikr. Anat.,* v. 60, 1902.

782. **Goette, A.** Entwick. der Teleostierkieme. *Zool. Anz.,* v. 1, 1878.

783. —— Über die Kiemen der Fische. *Zeitschr. f. wiss. Zool.,* v. 69, 1901.

784. **Greil, A.** Homologie der Anamnierkiemen. *Anat. Anz.,* 28, 1906.

785. **Harrison, R. G.** Devel. of Balancer in Amblystoma. *J. Exper. Zool.,* v. 41, 1925 (Bibl.).

786. **Jacobshagen, E.** Homologie der Wirbeltierkiemen. *Jen. Zeitschr. f. Naturw.,* v. 57, 1920.

787. **Kastschenko, N.** Schicksal d. Schlundspalten b. Säugetieren. *Arch. mikr. Anat.,* v. 30, 1887.

788. —— Schlundspaltsystem des Hühnchens. *Arch. Anat. u. Phys.,* 1887.

789. **Kellicott, W. E.** Devel. of Vascular System of Ceratodus. *Mem. Acad. Sci. New York,* 1905.

790. **Kerr, J. G.** Devel. of Lepidosiren paradoxa. *Phil. Trans.,* v. 192, 1900 ; *Quart. J. Micr. Sci.,* v. 46, 1902.

791. —— Devel. of Polypterus senegalus. *Budgett Mem. Vol.,* London, 1907.

792. **Lankester, E. R.,** and **Willey, A.** Devel. of Atrial Chamber of Amphioxus. *Quart. J. Micr. Sci.,* v. 31, 1890.

793. **Moroff, T.** Entw. der Kiemen bei Knochenfischen. *Arch. mikr. Anat.,* v. 60, 1902.

794. —— Entw. der Kiemen bei Fischen. *Arch. mikr. Anat.,* v. 64, 1904.

795. **Oppel, A.** Lehrb. d. vergl. mikr. Anat., v. 6, 1905.

796. **Orton, J. H.** Ciliary Mechanisms in Amphioxus, etc. *J. Mar. Biol. Ass.,* v. 10, 1913–15.

797. **Plehn, M.** Zum feineren Bau der Fishkeime. *Zool. Anz.,* v. 24, 1901.

798. **Regan, C. T.** A Classification of the Selachian Fishes. *Proc. Zool. Soc.,* 1906.

799. **Reiss, J. A.** Bau der Kiemblätter b. d. Knochenfischen. *Arch. f. Naturgesch.,* 47 Jahrg., 1881.

800. **Schulze, F. E.** Die inneren Kiemen der Batrachierlarven. *Abh. K. Preuss. Ac. Berlin*, 1888 and 1892.

801. **Stadtmüller, F.** Entw. u. Bau d. papillenf. Erhebungen a. d. Branchialbogen d. Salamandridenlarven. *Zeit. f. Morph. u. Anthr.*, v. 24, 1924.

CHAPTER X

VASCULAR SYSTEM, HEART

802. **Allis, E. P.** Pseudobranchial Circulation in Amia. *Zool. Jahrb.*, Abt. Anat., v. 14, 1900.

803. —— Pseudobr. and Carotid Arteries in Ameiurus. *Anat. Anz.*, v. 33, 1908.

804. —— In Chlamydoselachus. *Ibid.*, v. 39, 1911.

805. —— In Polyodon. *Ibid.*

806. —— In Esox, Salmo, Gadus, and Amia. *Ibid.*, v. 41, 1912.

807. **Ayers, H.** Morph. of Carotids (Chlamydoselachus). *Bull. Mus. Harvard*, v. 17, 1889.

808. **Beddard, F. E.**, and **Mitchell, P. C.** Heart of Alligator. *Proc. Zool. Soc.*, 1895.

809. **Bemmelen, J. F. van.** Halsgegend b. Reptilien. *Zool. Anz.*, v. 10, 1887.

810. **Benninghoff, A.** Anat. u. Entw. des Amphibienherzens. *Morph. Jahrb.*, v. 51, 1921.

811. **Boas, J. E. V.** Conus arteriosus b. Butirinus, etc. *Morph. Jahrb.*, v. 6, 1880.

812. —— Hertz und Arterienbogen bei Ceratodus und Protopterus. *Morph Jahrb.*, 6, 1880.

813. —— Conus art. u. Arterienbogen d. Amphibien. *Ibid.*, 7, 1882.

814. **Boveri, T.** Nierencanälchen des Amphioxus. *Zool. Jahrb.*, v. 5, 1892.

815. **Bremer, J. L.** I. Devel. of Heart: II. Left Aorta of Reptiles. *Am. J. Anat.*, v. 42, 1928.

816. **Bruner, H. S.** Heart of Lungless Salamanders. *J. Morph.*, v. 16, 1900.

817. —— Cephalic Veins and Sinuses of Reptiles. *Am. J. Anat.*, v. 7, 1907.

818. **Carazzi, O.** Sist. arterioso di Selache. *Anat. Anz.*, v. 26, 1905.

819. **Erdmann, B.** Entw. Atrioventrikularklappen bei den Anuren. *Morph. Jahrb.*, v. 51, 1921.

820. **Fuchs, F.** Entw. des Kiebitzherzens (Vanellus). *Z. f. Anat. u. Entw.*, v. 75, 1925.

821. **Gaupp, E.** Anat. des Frosches, 1896–1901.

822. **Gegenbaur, C.** Vergl. Anat. des Herzens. *Jen. Zeitschr. Naturw.*, v. 2, 1866.

823. —— Conus arteriosus der Fische. *Morph. Jahrb.*, v. 17, 1891.

824. **Gelderen, C. van.** Morph. d. Sinus durae matris. *Zeitschr. f. Anat. u. Entw.*, v. 73 and v. 74, 1924 ; v. 75, 1925.

825. **Goette, A.** *Entw. des Flussneunauges (Petromyzon)*, 1890.

826. **Goodrich, E. S.** On Reptilian Heart. *J. of Anat.*, v. 53, 1919.

827. **Granel, F.** Structure et dével. de la Pseudobranchie des Téléostéens. *C.R. Ac. Sci. Paris*, v. 175, 1922.

828. —— Signification morphologique de la pseudobranchie des Téléostéens. *Ibid.*, v. 175, 1922.

829. —— Étude histologique et embr. sur la pseudobranchie des Téléostéens. *Arch. d'Anat. Histol. et Embr.*, v. 2, 1923.

830. **Granel, F.** Sur la pseudobranchie de Chrysophrys. *C.R. Ass. des Anatomistes*, 1923.

831. **Greil, A.** Vergl. Anat. u. Entw. des Herzens u. d. Truncus art. der Wirbeltiere. *Morph. Jahrb.*, v. 31, 1903.

832. **Grosser, O.,** u. **Brezina, E.** Entw. d. Venen des Kopfes bei Reptilien. *Morph. Jahrb.*, v. 23, 1895.

833. **Hafferl, A.** Entwicklungsgech. der Kopfgefässe des Gecko (Platydactylus). *Anat. Hefte*, v. 59, 1921.

834. —— Entw. der Kopfarterien b. Kiebitz (Vanellus). *Ibid.*

835. **Hochstetter, F.** Entw. d. Blutgefässsystems. Hertwigs *Handb. Entw. Wirbeltiere*, v. 3, Jena, 1906 (Bibl.).

836. —— Blutgefässsyst. der Krocodile. Voeltzkow, *Reise in Ostafrika*, v. 4, 1906.

837. **Hopkins, G. S.** Heart of some Lungless Salamanders. *Am. Nat.*, 30, 1896.

838. **Hoyer, H.** Morphologie des Fischherzens. *Bull. intern. Acad. Sc. Cracovie*, 1900.

839. **Kern, A.** Das Vogelherz. *Morph. Jahrb.*, v. 56, 1926.

840. **Kerr, J. G.** Text-book of Embryology, vol. 2, London, 1919.

841. **Langer, A.** Entw. der Bulbus cordis bei Amphibien u. Reptilien. *Morph. Jahrb.*, v. 21, 1894.

842. —— bei Vögeln u. Säugetieren. *Ibid.*, v. 22, 1894.

843. **Lankester, E. R.** Hearts of Ceratodus, Protopterus, and Chimaera. *Trans. Zool. Soc.*, v. 10, 1878.

844. **Legros, R.** Appareil vasculaire de l'amphioxus. *Mitth. Zool. Sta. Neapel*, vol. 15, 1902.

845. **Lillie, F. R.** Devel. of Chick. New York, 1919.

846. **Marshall, A. M.,** and **Bles, E. J.** Devel. of Blood-vessels in Frog. Stud. Owens College, 1890.

847. **Masius, J.** Dével. du cœur chez le poulet. *Arch. de Biol.*, v. 9, 1889.

848. **Maurer, F.** Pseudobranchie der Knochenfische. *Morph. Jahrb.*, v. 9, 1884.

849. —— Kiemen u. i. Gefässe b. Amphibien u. Teleostiern. *Morph. Jahrb.*, v. 14, 1888.

850. **Mayer, P.** Entw. des Herzens, etc., bei Selachier. *Mitth. Zool. Sta. Neapel*, vol. 7, 1887.

851. **Müller, F. W.** Entw. u. morph. Bedeutung der Pseudobranchie bei Lepidosteus. *Arch. mikr. Anat.*, v. 49, 1897.

852. **O'Donoghue, C. H.** Blood Vascular Syst. of Sphenodon. *Phil. Trans. Roy. Soc.*, B, v. 210, 1920 (Bibl.).

853. **Parker, T. J.** Blood-vessels of Mustelus. *Phil. Trans. Roy. Soc.*, B, v. 177, 1886.

854. **Parker, W. N.** Anat. and Phys. of Protopterus annectens. *Trans. Irish Acad.*, v. 30, 1892.

855. **Platt, J. R.** Morph. of Vertebrate Head. *J. of Morph.*, v. 5, 1891.

856. **Raffaele, D. F.** Sviluppo d. sist. vascolare n. Selacei. *Mitt. Zool. Sta. Neapel*, v. 10, 1892.

857. **Rao, C. R. N.,** and **Ramana, R. S.** Conus arteriosus of Engystomatidae, etc. *Proc. Zool. Soc. London*, 1926.

858. **Rau, A. S.** Heart, etc., of Ceratophrys. *J. of Anat.*, v. 58, 1924.

859. —— Heart of Tiliqua and Eunectes. *J. of Anat.*, v. 59, 1924.

860. **Ridewood, W. G.** Circulus Cephalicus in Teleostean Fishes. *Proc. Zool. Soc.*, 1899.

861. **Robertson, J. I.** Devel. of Heart of Lepidosiren. *Quart. J. Micr. Sci.*, v. 59, 1913.

862. **Röse, C.** Beitr. z. vergl. Anat. d. Herzens. *Morph. Jahrb.*, v. 16, 1890.

863. **Rückert, J.** Anlage d. Herzens, etc., b. Selachierembryonen. *Biol. Centrabl.*, v. 8, 1888.

864. **Sabatier, A.** Syst. aortique d. la série des Vertébrés. *Ann. Sc. Nat. Zool.*, v. 19, 1874.

865. —— Études sur le cœur, etc., des Vertébrés. Montpellier, 1873.

866. **Salzer, H.** Entw. d. Kopfvenen der Meerschweinchens. *Morph. Jahrb.*, v. 23, 1895.

867. **Sappey, Ph. C.** L'appareil mucipare et sur le syst. lymphatique des poissons. Paris, 1880.

868. **Senior, H. D.** Conus arteriosus in Tarpon. *Biol. Bull.*, v. 12, 1907.

869. **Sewertzoff, A. N.** Entwickl. der Kiemen u. Kiemenbogengefässe. *Zeitschr. wiss. Zool.*, v. 121, 1923.

870. **Shiino, T.** Arteriellen Kopfgefässe d. Reptilien. *Anat. Hefte,* v. 51, 1914.

871. **Smith, W. C.** Conus arteriosus in Teleosts. *Anat. Rec.*, v. 15, 1918.

872. **Spencer, W. B.** Ceratodus. The Blood-vessels. *Macleay Memorial Vol.*, 1892.

873. **Stöhr, Ph.** Klappenapparat in Conus arteriosus der Selachier u. Ganoiden. *Morph. Jahrb.*, v. 2, 1876.

874. **Takahashi, So.** Formation of Cardiac Septa in Chick. *J. of Anat.*, v. 57, 1923.

875. **Tandler, J.** Vergl. Anat. d. Kopfarterien b. d. Mammalia. *Denkschr. k. Akad. d. Wiss.*, 67, Wien, 1899.

876. —— Entw. d. Kopfarterien b. d. Mammalia. *Morph. Jahrb.*, 30, 1902.

877. —— Vergl. Anat. d. Kopfarterien b. d. Mammalia. *Anat. Hefte*, v. 18, 1902.

878. **Twining, G. H.** Embryonic History of Carotid Arteries in the Chick. *Anat. Anz.*, v. 29, 1906.

879. **Vialleton, L.** Cœur des lamproies. *Arch. d'anat. Micr.*, v. 6, 1903.

880. **Vialli, M.** Branchie e pseudobranchie d. Sturione. *Publ. Staz. Zool. Napoli*, v. 5, 1925.

881. —— Le pseudobranchie dei pesci. *Arch. Ital. Anat. e Embr.*, v. 23, 1926.

882. **Wright, R. R.** On the Hyomandibular Clefts and Pseudobranchs of Lepidosteus and Amia. *J. Anat. and Phys.*, v. 19, 1885.

CHAPTER XI

AIR-BLADDER AND LUNGS

883. **Aeby, Ch.** Bronchialbaum d. Säugetiere. Leipzig, 1880.

884. **Anton, W.** Nasenhöhle der Perennibranchiaten. *Morph. Jahrb.*, v. 44, 1922.

885. **Assheton, R.** Devel. of Gymnarchus. *Budgett Mem. Vol.*, 1907.

886. **Ballantyne, F. M.** Air-bladder and Lungs. *Tr. Roy. Soc. Edin.*, v. 55, 1927.

887. **Beaufort, L. F. de.** Schwimmblase der Malacopterygii. *Morph. Jahrb.*, v. 39, 1909.

888. **Bloch, L.** Schwimmblase, Knochenkapsel and Weber'scher Apparat von Nemachilus. *Jen. Zeit. f. Naturw.*, 34, 1900.

889. **Bohr, C.** Infl. of Section of Vagus n. on Gases in Air-bladder. *J. of Physiol.*, v. 15, 1894.

890. **Bremer, J. L.** Lung of Opossum. *Am. J. of Anat.*, v. 3, 1904.

891. **Bridge, T. W.**, and **Haddon, A. C.** Air-bladder and Weberian Ossicles of Siluroid Fishes. *Phil. Trans. Roy. Soc.*, B, v. 184, 1893 (Bibl.).

892. **Bruner, H. L.** Pulmonary Respir. in Amphibians. *Morph. Jahrb.*, v. 48, 1914.

893. **Camerano, L.** Ric. anat.-fisiol. i. a. Salamandrini apneumoni. *Anat. Anz.*, v. 9, 1894 ; v. 12, 1896.

894. **Campana, J. C.** Phys. de la respiration chez les oiseaux. Paris, 1875.

895. **Coggi, A.** Blutdrüsen i. d. Schwimmblase d. Hechtes. *Morph. Jahrb.*, v. 15, 1889.

896. **Corning, H. K.** Wundernetzbild. i. d. Schwimmblasen. *Morph. Jahrb.*, v. 14, 1888.

897. **Evans, H. M.** Anat. and Phys. of Air-bladder and Weberian Ossicles in Cyprinidae. *Proc. Roy. Soc.*, B, v. 97, 1925.

898. **Evans, H. M.**, and **Damant, G. C. C.** Physiol. of Swim-bladder in Cyprinoid Fishes. *Brit. J. Exper. Biol.*, v. 6, 1928.

899. **Fischer, G.** Bronchialbaum d. Vögel. *Zoologica*, v. 19, 1905 (Bibl.).

900. **Flint, J. M.** Devel. of Lungs. *Am. J. of Anat.*, v. 6, 1906.

901. **Goette, A.** Ursprung der Lungen. *Zool. Jahrb.*, v. 21, Anat., 1905.

902. **Göppert, E.** Schwimmblase, Lunge u. Kehlkopf. Hertwig's *Handb. Vergl. Entw. d. Wirbeltiere*, v. 2, 1902 (Bibl.).

903. **Greil, A.** Frage n. d. Ursprunge der Lungen. *Anat. Anz.*, 26, 1905.

904. **Guillot, N.** App. de la respiration dans les oiseaux. *Ann. Sc. Nat.*, v. 5 (3), 1846.

905. **Guyénot, E.** Étude de la vessie natatoire des Cyprinides. *C.R. Soc. Biol. Paris*, 1905.

906. **Haldane, J. S.** Secret. and Absorpt. of Gas in Swim-bladder. *Science Progr.*, v. 7, 1898.

907. **Hall, F. G.** Functions of Swim-bladder. *Biol. Bull.*, v. 47, 1924 (Bibl.).

908. **Hardiviller, A. d'.** Ramif. bronchique chez le lapin. *Bibliogr. Anat.*, v. 4, 1896 ; v. 5, 1897.

909. **Hesser, K.** Entw. d. Reptilienlunge. *Anat. Hefte*, v. 29, 1905.

910. **Huntington, G. S.** Pulmonary Evol. of Mammalia. *Am. J. of Anat.*, v. 27, 1920 (Bibl.).

911. **Huxley, T. H.** Respiratory Organs of Apteryx. *Proc. Zool. Soc. London*, 1882.

912. **Juillet, A.** Poumon des oiseaux. *Arch. Zool. Exp. et Gén.*, v. 9, 1912 (Bibl.).

913. **Justesen, P. Th.** Entw. u. Verz. d. Bronchialbaumes. *Arch. mikr. Anat. u. Entw.*, v. 56, 1900.

914. **Kerr, J. G.** Devel. of Alim. Canal in Lepidosiren and Protopterus. *Quart. J. Micr. Sci.*, v. 54, 1910.

915. **Larsell, O.** Recurrent Bronchi of Air-sacs of Chick. *Anat. Anz.*, v. 47, 1914.

916. **Locy, W. A.**, and **Larsell, O.** Embryology of the Bird's Lung. Pt. 1, *Am. J. Anat.*, v. 19, 1916; Pt. 2, *Am. J. Anat.*, v. 20, 1916.

917. **Lühe, M.** Lungenlose Urodelen. *Zool. Zentralbl.*, v. 7, 1900.

918. **Makuschok, M.** Phylog. Entw. der Lungen. Pt. 1, *Anat. Anz.*, v. 39, 1911; Pt. 2, *Anat. Anz.*, v. 42, 1912.

919. **Makuschok, M.** Genetische Beziehung zwischen Schwimmblase u. Lungen. *Anat. Anz.*, v. 44, 1913.

920. **Milani, A.** Reptilienlunge. *Zool. Jahrb.*, Abt. Anat., v. 7, 1894; v. 10, 1897.

921. **Moser, F.** Entw. d. Wirbeltierlunge. *Arch. mikr. Anat. u. Entw.*, v. 60, 1902.

922. —— Entwickl. der Schwimmblase. *Anat. Anz.*, 23, 1903.

923. **Müller, B.** Air-sacs of Pigeon. *Smithsonian Misc. Publ.*, 1724, 1908.

924. **Narath, A.** Entw. d. Lunge v. Echidna. *Denkschr. Med. Nat. Ges. Jena*, v. 5, 1896.

925. —— Bronchialbaum d. Säugetiere. *Bibl. Medica*, 1901.

926. **Neumayer, L.** Entw. des Darmkanales, etc., b. Ceratodus. *Denkschr. Med. Nat. Ges. Jena*, v. 4, 1904.

927. **Nusbaum, J.** Gehörorgän u. Schwimmblase b. d. Cyprinoiden. *Zool. Anz.*, v. 4, 1881.

928. —— Gasdrüse u. Oval. *Anat. Anz.*, v. 31, 1907.

929. **Parker, T. J.** Air-bladder and Audit-organ in Red Cod. *Tr. New Z. Inst.*, v. 15, 1882.

930. **Piper, H.** Entw. u. Leber, Pankreas, Swimmblase u. Milz von Amia. *Anat. Anz.*, 21, 1902.

931. **Potter, G. E.** Respiratory Function of Swim-bladder in Lepidosteus. *J. Exp. Zool.*, v. 49, 1927.

932. **Rauther, M.** Vergl. Anat. der Swimmblase der Fische. *Ergeb. u. Fortschr. der Zool.*, v. 5, 1923 (Bibl.).

933. **Reiss, K.,** and **Nusbaum, J.** Histol. d. Gasdrüse i. d. Schwimmblase. *Anat. Anz.*, v. 27, 1905; v. 28, 1906.

934. **Ridewood, W. G.** The Air-bladder and Ear of Brit. Clupeoid Fishes. *Journ. Anat. and Phys.*, v. 26, 1891.

935. **Robinson, A.** Devel. of Lungs of Rats and Mice. *J. of Anat. and Physiol.*, v. 23, 1889.

936. **Roché, G.** Anat. comp. des réservoirs aériens chez les oiseaux. *Ann. d. Sc. Nat. Zool.*, v. 11 (7), 1891.

937. **Rösler, H.** Erste Anlage der Lungen u. d. Nebengekröse einiger Vogelarten. *Anat. Hefte*, 1te Abt., v. 44, 1911.

938. **Rowntree, W. S.** Visceral Anatomy of Characinidae, etc. *Trans. Linn. Soc.*, v. 9, 1903.

939. **Sörensen, W.** Air-bladder and Weberian Ossicles. *J. Anat. and Phys.*, v. 29, 1895.

940. **Spencer, W. B.** Bau d. Lungen v. Ceratodus u. Protopterus. *Denkschr. Med. Nat. Ges. Jena*, v. 4, 1898.

941. **Spengel, J. W.** Schwimmblasen, Lungen u. Kiementaschen. *Zool. Jahrb.*, Suppl. 7, 1904.

942. **Tracy, H. C.** Morph. of Swim-bladder in Teleosts. *Anat. Anz.*, v. 38, 1911.

943. —— Clupeoid Cranium in its Relation to the Swim-bladder, etc. *J. of Morph.*, 33, 1920.

944. **Vincent, S.,** and **Barnes, S. A.** Red Glands in Swim-bladder. *J. Anat. and Phys.*, v. 30, 1896.

945. **Weber, A.,** et **Buvignier, A.** Dével. de l'app. pulmonaire chez Miniopterus. *Bibl. Anat.*, v. 12, 1903. Chez le canard, etc. *C.R. Soc. Biol.*, v. 55, 1903.

946. Wiedersheim, R.   Kehlkopf der Ganoiden u. Dipnoer.   *Anat. Anz.*, v. 22, 1903.

947. Wilder, H. H.   Amphibian Larynx.   *Zool. Jahrb.*, Abt. Anat., v. 9, 1896.

948. —— Lungless Salamanders.   *Anat. Anz.*, v. 9, 1894 ; v. 12, 1896.

949. Woodland, W. N. F.   Structure and Function of Gas Glands, etc.   *Proc. Zool. Soc. London*, 1911.

950. —— Physiol. of Gas Production.   *Anat. Anz.*, v. 40, 1912.

951. Wright, R. R.   Skull and Auditory Organ of Siluroid Hypophthalmus.   *Trans. R. Soc. Canada*, Sect. 4, 1885.

CHAPTER XII

Subdivision of Coelom, and Diaphragm

952. Beddard, F. E.   Diaphragm and Muscular Anat. of Xenopus, etc., Anat. of Pipa.   *Proc. Zool. Soc.*, 1895.

953. —— Struct. and Classif. of Birds.   London, 1898.

954. Bertelli, D.   Pieghe d. reni primitivi.   Pisa, 1897.

955. —— Rich. di embriol. e di anat. comp. sul diaframma e sull' apparechio respiratorio.   *Arch. di Anat. e di Embr.*, v. 4, 1905.

956. Brachet, A.   Dével. de la cavité hépato-entérique, etc.   *Arch. de Biol.*, v. 13, 1895 ; *Anat. Anz.*, v. 11, 1896.

957. —— Dével. du diaphragme et du foie.   *J. de l'Anat. et Physiol.*, 1895 and 1897.

958. —— Entwickl. d. g. Körperhöhlen u. Entwickl. d. Zwerchfells.   *Ergeb. Anat. u. Entw.*, v. 7, 1897 (Bibl.).

959. Broman, I.   Entw. der Bursa omentalis.   Wiesbaden, 1904 (Bibl.).

960. —— Entw. d. Membr. peric. u. d. Zwerchfells.   *Ergeb. Anat. u. Entw.*, v. 20, 1911 (Bibl.).

961. Brouha, M.   Dével. du foie, etc., chez les oiseaux.   *J. de l'Anat. et Physiol.*, 1898.

962. Butler, G. W.   Subdiv. of Body-cavity in Lizards, Crocodiles, and Birds.   *Proc. Zool. Soc. London*, 1889.   In Snakes.   *Ibid.*, 1892.

963. —— Suppression of the Right Lung in *Amphisbaenidae* and of Left Lung in Snakes, Lizards, and Amphibians.   *Proc. Zool. Soc.*, 1895.

964. Goette, A.   Entwick. des Flussneunauges (Petromyzon).   *Abh. z. Entw. der Tiere*, 5tes Heft, 1890.

965. Goodrich, E. S.   Devel. of Peric.-peritoneal Canals in Selachians.   *J. of Anat.*, v. 53, 1918.

966. Gössnitz, W. v.   Diaphragmafrage.   *Denkschr. Med. Nat. Ges. Jena*, v. 4, 1901.

967. Hochstetter, F.   Scheidewandbild., etc., b. Sauriern.   *Morph. Jahrb.*, v. 27, 1899.

968. —— Scheidewand zw. peric. u. Peritoneal-höhle v. Acanthias.   *Morph. Jahrb.*, v. 29, 1900.

969. —— Scheidewandbild. i. d. Krocodile.   Voeltzkow, *Reise Ostafrika*, v. 4, 1906.

970. Keith, A.   Mammalian Diaphragm and Pleural Cavities.   *J. Anat. and Phys.*, v. 39, 1905.

971. Lockwood, C. B.   Devel. of Pericardium, Diaphragm, etc.   *Phil. Trans. R.S.*, v. 179, 1888.

972. **Mall, F. P.** Devel. of Human Diaphragm. *Proc. Assoc. Am. Anatomists,* 1900.

973. **Mathes, P.** Morph. d. Mesenterialbildungen b. Amphibien. *Morph. Jahrb.,* v. 53, 1895.

974. **Poole, M.** Subdiv. of Pleuro-perit. Cav. in Birds. *Proc. Zool. Soc.,* 1909.

975. **Ravn, E.** Bild. d. Scheidewand in Säugetier. *Arch. f. Anat. u. Entw.,* 1889.

976. —— Entw. d. Zwerchfells, etc. *Ibid.,* Suppl. 1889.

977. —— Bild. d. Septum transversum. *Ibid.,* 1896.

978. **Swaen, A.** Dével. du foie, etc. *J. de l' Anat. et Physiol.,* 1896–97.

979. **Uskow, N.** Entw. d. Zwerchfelles, etc. *Arch. f. mikr. Anat.,* v. 22, 1883.

CHAPTER XIII

EXCRETORY ORGANS AND GENITAL DUCTS

980. **Allen, B. M.** Devel. of Ovary and Testis of Mammals. *Am. J. Anat.,* v. 3, 1904.

981. —— Rete-cords and Sex-cords of Chrysemys. *Ibid.,* v. 5, 1905.

982. **Audigé, J.** Reins des Téléostéens. *Arch. Zool. Expér.,* v. 4, 1910.

983. **Ayers, H.** Beitr. z. Anat. u. Phys. der Dipnoër. *Jen. Zeitschr.,* v. 18, 1884.

984. —— Pori abdominales. *Morph. Jahrb.,* v. 10, 1885.

985. **Balfour, F. M.** Comparative Embryology. v. 2, London, 1881.

986. **Ballantyne, F. M.** Male Genito-urinary Organs of Ceratodus. *Proc. Zool. Soc. London,* 1928.

987. **Bates, G. E.** Pronephric Duct in Elasmobranchs. *J. Morph.,* v. 25, 1914.

988. **Beard, J.** Origin of Segmental Duct. *Anat. Anz.,* v. 2, 1887.

989. —— Pronephros of Lepidosteus. *Anat. Anz.,* v. 10, 1894.

990. **Bles, E. S.** Openings in Wall of Body-cavity. *Proc. Roy. Soc.,* 1897.

991. **Borcéa, J.** Syst. uro-génital des Élasmobranches. *Arch. Zool. exp. et gén.,* v. 4, 1905.

992. **Boyden, E. A.** Devel. of Cloaca in Ostrich. *Anat. Rec.,* v. 24, 1922. Devel. of Avian Cloaca. *J. Exper. Zool.,* v. 46, 1924.

993. **Brachet, A.** Embryologie des vertébrés. Paris, 1921.

994. **Brambell, F. W. R.** Devel. and Morph. of Gonads of Mouse. *Proc. Roy. Soc. London,* B, v. 102, 1927.

995. **Brauer, A.** Entw. u. Anat. der Gymnophionen III. : Entw. der Excretionsorgane. *Zool. Jahrb.,* Abt. Anat., v. 16, 1902.

996. **Bridge, T. W.** Pori abdominales. *Jour. Anat. and Phys.,* v. 14, 1879.

997. **Brock, A. J. P. v. d.** Urogenitalapp. der Beutler, etc. *Morph. Jahrb.,* v. 41, 1910.

998. **Brock, J.** Geschlechtsorgane der Knochenfische. *Morph. Jahrb.,* 4, 1878.

999. —— Geschlechtsorgane e. Muraenoiden. *Mitth. Zool. Sta. Neapel,* v. 2, 1881.

1000. **Burlend, T.** Pronephros of Chrysemys. *Zool. Jahrb.,* Abt. Anat., v. 36, 1913 ; v. 37, 1914.

1001. **Conel, J. Lek.** Urogenital System of Myxinoids. *J. Morph.,* v. 29, 1917.

1002. **Dean, B.** Larval Devel. of Amia. *Zool. Jahrb.,* Abt. Syst., v. 9, 1897.

1003. Dean, B. Embryology of Bdellostoma. *Festschr. f. C. v. Kupffer*, 1899.

1004. Essenberg, J. M. Sex-differentiation in Xiphophorus. *Biol. Bull.*, v. 45, 1923.

1005. Felix, W. Entw. des Harnapparates. Hertwig's *Handb. Entw. d. Wirbeltiere*, v. 3, Jena, 1906.

1006. —— Devel. of Urinogenital Organs. V. 2, Keibel and Mall, *Human Embryology*, 1912.

1007. Felix, W., u. Bühler, A. Entw. d. Keimdr. u. i. Ausführgänge. Hertwig's *Handb. Entw. d. Wirbeltiere*, v. 3, Jena, 1906.

1008. Field, H. H. Devel. of Pronephros and Segmental Duct in Amphibia. *Bull. Harv. Mus. Comp. Zool.*, v. 21, 1891.

1009. Fleischmann, A. Morph. Stud. ü. Kloake, etc. (Mammalia). *Morph. Jahrb.*, v. 32, 1903.

1010. Fraser, E. A. Devel. of Urogenital Syst. in Marsupialia. *J. of Anat.*, v. 53, 1918. Pronephros and Mesonephros in Cat. *J. of Anat.*, v. 54, 1920.

1011. —— Devel. of Pronephros of Acipenser. *Quart. J. Micr. Sci.*, v. 71, 1928 (Bibl.).

1012. Fürbringer, M. Entw. d. Amphibienniere, Heidelberg, 1877. Anat. u. Entw. d. Exkretionsorg. *Morph. Jahrb.*, v. 4, 1878.

1013. Gemmill, J. F. Entsteh. d. Müller's Ganges b. Amphibien. *Arch. Anat. u. Embr.*, 1896.

1014. Gerhardt, U. Entw. d. bleib. Niere. *Arch. mikr. Anat.*, v. 57, 1901.

1015. —— Kopulationsorgane d. Säugetiere. *Jen. Zeitschr.*, v. 39, 1905.

1016. Goodrich, E. S. Coelom, Genital Ducts, and Nephridia. *Quart. J. Micr. Sci.*, v. 37, 1895.

1017. —— Excretory Organs of Amphioxus. *Quart. J. Micr. Sci.*, v. 45, 1902.

1018. Guitel, F. Anat. des reins des Gobiésocidés. *Arch. Zool. Expér.*, v. 5, 1906.

1019. Hall, R. W. Devel. of Mesonephros and Müllerian Ducts in Amphibia. *Bull. Mus. Comp. Zool. Harvard*, vol. 45, 1904.

1020. Haller, B. Ovarialsack der Knochenfische. *Anat. Anz.*, v. 27, 1905.

1020a. Hatta, S. Devel. of Pronephros, etc., in Petromyzon. *J. Coll. Sc. Imp. Univ. Tokyo*, v. 13, 1900.

1021. Helmuth, K. Morph. Stud. ü. Kloake, etc. (Chelonia, Crocodilia). *Morph. Jahrb.*, v. 30, 1902.

1022. Hoffmann, C. K. Entw. d. Urogen.-Organe b. Anamniern. *Zeitschr. wiss. Zool.*, v. 44, 1886 ; b. Reptilien. *Ibid.*, v. 48, 1889.

1023. Holzbach, E. Die Hemmungsbildungen der Müllerschen Gänge. *Beitr. Geburtsb. Gynäkol.*, v. 14, 1909.

1024. Huxley, T. H. Oviducts of Osmerus, etc. *Proc. Zool. Soc.*, 1883.

1025. Hyrtl, J. Morph. der Urogenital-Organe der Fische. *Denk. Ak. Wien*, v. 1, 1850.

1026. —— Geschlechts- und Harnwerkzeuge b. d. Ganoiden. *Denk. Ak. Wien*, v. 8, 1854.

1027. Janosik, J. Embr. d. Urogenitalsyst. *Sitz. Ber. Akad. Wiss. Wien*, v. 91, 1885 ; v. 109, 1890.

1028. Jungersen, H. F. E. Entw. der Geschlechtsorgane bei der Knochenfischen. *Arb. Zool. Inst. Würzburg*, v. 9, 1889.

1029. Jungersen, H. F. E. Embryonalniere des Störs. *Zool. Anz.*, v. 16, 1893. Embryonalniere von *Amia calva*. *Ibid.*, v. 17, 1894. Urogenital-organe v. Polypterus u. Amia. *Ibid.*, v. 23, 1900.

1030. Keibel, F. Entw. des Urogenitalapparates von Echidna. *Denkschr. Med. Nat. Ges. Jena*, v. 6, 1904.

1031. Kerens, B. Dével. de l'app. excréteur des Amniotes. *Arch. de Biol.*, v. 22, 1907.

1032. Kerr, J. G. Male Genito-urinary Organs of Lepidosiren and Protopterus. *Proc. Zool. Soc.*, 1901 ; *Proc. Philos. Soc. Cambridge*, v. 11, 1902.

1033. —— Devel. of Polypterus. *Budgett Mem. Vol.*, London, 1907.

1034. Kirkaldy, J. W. Head Kidney of Myxine. *Quart. J. Micr. Sci.*, v. 35, 1894.

1035. Lickteig, A. Geschlechtsorgane der Knochenfische. *Zeitschr. wiss. Zool.*, v. 106, 1913.

1036. Maas, O. Vorniere u. Urniere bei Myxine. *Zool. Jahrb.*, Abt. Anat., v. 10, 1897.

1037. MacBride, E. W. Devel. of Oviduct in Frog. *Quart. J. Micr. Sci.*, v. 33, 1892.

1038. MacLeod. Appareil reprod. femelle des Téléostéens. *Arch. Biol.*, v. 2, 1881.

1039. Martin, A. Anlage d. Urniere b. Kaninchen. *Arch. mikr. Anat.*, v. 32, 1888.

1040. Maschkowzeff, A. Zur Phylogenie d. Urogenitalsystems der Wirbeltiere (Acipenser). *Zool. Jahrb.*, Abt. Anat., v. 48, 1926.

1041. Milhalkovics, v. Entw. d. Harn- u. Geschlechtsapp. d. Amnioten. *Intern. Monatsschr. Anat. u. Phys.*, v. 2, 1885.

1042. Moens, N. W. I. Peritonealkanäle der Schildkröton u. Krokodile. *Morph. Jahrb.*, v. 44, 1911.

1043. Mollier, S. Vornierensyst. bei Amphibien. *Arch. Anat. u. Entw.*, 1890.

1044. Nussbaum, J. Entw. samenbl. Wege b. Anuren. *Zool. Anz.*, v. 3, 1880.

1045. —— Wimpertricher i. d. Niere d. Anuren. *Ibid.*

1046. Pomayer, C. Morph. Stud. ü. Kloake, etc., Vögel. *Morph. Jahrb.*, v. 30, 1902.

1047. Price, G. C. Devel. of Excretory Organs in Bdellostoma. *Zool. Jahrb.*, Abt. Anat., v. 10, 1897 ; *Amer. Journ. Anat.*, v. 4, 1904.

1048. Rabl, C. Entw. d. Urogenitalsystems der Selachier. *Morph. Jahrb.*, v. 24, 1896.

1049. Rabl, H. Vorniere u. Bildung des Müller'schen Ganges bei Salamandra, etc. *Arch. mikr. Anat.*, v. 64, 1904.

1050. Rückert, J. Über d. Entsteh. d. Exkretionsorgane bei Selachiern. *Arch. Anat. u. Entw.*, 1888.

1051. —— Entw. d. Exkretionsorgane. *Anat. Hefte, Ergeb.*, 1892.

1052. Schneider, G. Entw. der Genitalcanäle bei Cobitis u. Phoxinus. *Mém. Acad. Imp. St-Pétersb.*, v. 11, 1895.

1053. Schreiner, K. E. Entw. der Amniotenniere. *Zeitschr. f. wiss. Zool.*, vol. 71, 1902.

1054. Scott, W. B. Beitr. z. Entw. Gesch. der Petromyzonten. *Morph. Jahrb.*, v. 7, 1881. Development of Petromyzon. *Jour. Morph.*, v. 1, 1887.

1055. Sedgwick, A. Head Kidney in Chick. *Quart. J. Micr. Sci.*, v. 19, 1879 ; v. 20, 1880.

1056. —— Early Devel. of Wolffian Duct, etc. *Quart. J. Micr. Sci.*, v. 21, 1881.

1057. Semon, R. Keimdrüse b. Hühnchen, etc. *Jen. Zeitschr.*, v. 21, 1887.
1058. —— Morph. Bedeut. d. Urniere. *Anat. Anz.*, v. 5, 1890.
1059. —— Bauplan d. Urogenitalsyst. *Jen. Zeitschr. Nat.*, v. 19, 1891.
1060. —— N. ü. d. Zusammenhang der Harn- u. Geschlechtsorgane b. d. Ganoiden. *Morph. Jahrb.*, v. 17, 1891.
1061. —— Exkretionsystem der Myxinoiden. *Festschr. f. C. Gegenbaur*, v. 3, Leipzig, 1896.
1062. —— Urogenitalsyst. d. Dipnoer. *Zool. Anz.*, v. 24, 1901.
1063. Semper, C. Urogenitalsystem der Selachier. *Arb. Inst. Würzburg*, v. 2, 1875.
1064. Spengel, J. W. Urogenitalsyst. der Amphibien. *Arb. Zool. Inst. Würzburg*, v. 3, 1876.
1065. —— Exkretionsorg. b. Myxine. *Anat. Anz.*, v. 13, 1897.
1066. Swaen, A., et Brachet, A. Dével. du mésoblaste du Téléostéens. *Arch. de Biol.*, v. 16, 1899 ; v. 18, 1901.
1067. Waldeyer, W. Eierstock u. Ei. Leipzig, 1870.
1068. Walsche, L. de. Dével. du pro- et mésonéphros des Chéloniens. *Arch. de Biol.*, v. 39, 1929.
1069. Weber, M. Abdominalporen der Salmoniden. *Morph. Jahrb.*, v. 21, 1887.
1070. Weldon, W. F. K. Head-kidney of Bdellostoma. *Quart. J. Micr. Sci.*, v. 24, 1884.
1071. —— Early Devel. of Lacerta. *Quart. J. Micr. Sci.*, v. 31, 1890.
1072. Wheeler, W. M. Devel. of Urogenitalorgans of Lamprey. *Zool. Jahrb. Anat.*, v. 13, 1899.
1073. Wijhe, J. W. v. Mesodermsegmente des Rumpfes u. d. Entw. d. Exkretionssyst. *Arch. f. mikr. Anat.*, v. 23, 1889.
1074. Wilson, G. Devel. of Ost. Abdom. in Crocodile. *Trans. Roy. Soc. Edin.*, v. 38, 1897.
1075. —— Devel. Müll. Duct of Amphibians. *Ibid.*
1076. Winiwarter, H. v. Corps de Wolff et dével. du canal de Müller. *Arch. de Biol.*, v. 25, 1910.

CHAPTER XIV

PERIPHERAL NERVOUS SYSTEM AND SENSE ORGANS

1077. Abel, W. Devel. of Symp. n. s. in Chick. *J. of Anat. and Phys.*, v. 46, 1912 ; v. 47, 1913.
1078. Adelmann, H. B. Devel. of Neural Folds and Cranial Ganglia of Rat. *J. Comp. Neur.*, v. 39, 1925.
1079. Agar, W. E. Spiracular Gill Cleft in Lepidosiren and Protopterus. *Anat. Anz.*, v. 28, 1906.
1080. Alcock, R. Peripheral Distribution of Cranial Nerves of Ammocaetes. *J. Anat. and Phys.*, v. 33, 1898–99.
1081. Allis, E. P., Jr. Anat. and Devel. of the Lateral Line System in Amia. *Jour. Morph.*, ii., 1889.
1082. —— Lateral Sensory Canals of *Polypterus*. *Anat. Anz.*, 17, 1900.
1082a. —— Lat. Sensory Canals, etc., of Mustelus. *Quart. J. Micr. Sci.*, v. 45, 1901.
1083. —— Lateral Canals and Cranial Bones of Polyodon folium. *Zool. Jahrb.*, Abt. Anat., 17, 1903.

1084. **Allis, E. P., Jr.** Lat. Sensory System in *Muraenidae*. *Int. Monat. Anat. u. Phys.*, v. 20, 1903.

1085. —— Latero-sensory Canals and related Bones in Fishes. *Intern. Mon. An. Phys.*, v. 21, 1905.

1085a. —— Lat. Sens. Canals of Plagiostomi. *J. Comp. Neur.*, v. 35, 1922.

1086. **Ayers, H.** Morph. of Vertebrate Ear. *Jour. Morph.*, v. 6, 1892.

1087. **Ayers, H.,** and **Worthington, J.** Skin End-organs of Trigeminus and Lateralis Nerves of Bdellostoma. *Am. J. of Anatomy*, v. 7, 1907.

1088. **Beard, J.** Sense Organs of Lateral Line and Morph. of Vert. Auditory Organ. *Zool. Anz.*, v. 7, 1884.

1089. —— Branchial Sense Organs and their Associated Ganglia in Ichthyopsida. *Quart. J. Micr. Sci.*, v. 26, 1885.

1090. **Belogolowy, J.** Entw. d. Kopfnerven der Vögel. *Bull. Soc. Imp. Nat. Moscou*, v. 22, (1908) 1910.

1091. **Bemmelen, J. F. van.** Rudimentäre Kiemenspalten bei Elasmobranchiern. *Mitth. Zool. Sta. Neapel*, v. 6, 1885.

1092. **Bender, O.** Schleimhautnerven d. Facialis Glossopharyngeus u. Vagus. *Denk. Med. Nat. Ges. Jena*, v. 7, 1907.

1093. **Brandt, W.** Darmnervensyst. v. Myxine. *Zeitschr. f. Anat. u. Entw.*, v. 65, 1922.

1094. **Brauer, A.** Entw. u. Anat. d. Gymnophionen. *Zool. Jahrb.*, v. 7, Suppl., 1904.

1095. **Camus, R.** Entw. d. symp. Nervensyst. b. Frosch. *Arch. mikr. Anat.*, v. 81, 1913.

1096. **Chevrel, R.** Syst. nerveux grand sympathique des Élasmobranches et poissons osseux. *Arch. Zool. Exp. et Gén.*, v. V., Suppl., 1887.

1097. **Chiarugi, G.** Dével. des nerfs vague, etc. *Arch. Ital. Biol.*, v. 13, 1890.

1098. **Coghill, G. E.** Afferent Syst. of Head of Amblystoma. *J. Comp. Neur.*, 25, 1916.

1099. **Cole, F. J.** Cranial Nerves of Chimaera monstrosa. *Trans. R. Soc. Edin.*, v. 38, 1896.

1099a. —— Of Gadus. *Trans. Linn. Soc. London, Zool.*, v. 7, 1893.

1100. **Collinge, W. E.** Sensory Canal System of Fishes. Pt. I. Ganoidei. *Quart. J. Micr. Sci.*, v. 36, 1894.

1101. —— Sensory and Ampullary Canals of Chimaera. *Proc. Zool. Soc.*, 1895.

1102. **Cook, M. H.,** and **Neal, H. V.** Are Taste-buds of Elasmobr. of Endod. Origin? *J. Comp. Neur.*, v. 33, 1921.

1103. **Dogiel, A. S.** Darmgeflechte b. d. Säugetiere. *Anat. Anz.*, v. 10, 1895. Sympathischer Nervenzellen. *Ibid.*, v. 11, 1896. Geflechten des Darmes. *Arch. Anat. u. Phys.*, Anat. Abt., 1899.

1104. —— Periphere Nervensystem des Amphioxus. *Anat. Hefte*, 1. Abt., v. 21, 1903.

1105. **Dohrn, A.** Stud. z. Urgesch. d. Wirbeltierkörpers. 9, Unpaaren Flosse. *Mitt. Zool. Sta. Neapel*, v. 6, 1885. 13, Ammocaetes u. Petromyzon. 14, Rückenmarksnerven b. Selachiern. *Ibid.*, v. 7, 1888. 15, Metamerie des Kopfes. *Ibid.*, v. 9, 1890. 16, Entw. d. Augenmuskelnerven, v. 10, 1891. 18-22, Occipitalsomite, etc. *Ibid.*, v. 15, 1901-2.

1106. **Escher, K.** Seitenorgane u. i. Nerven C. Übergang z. Landleben. *Acta Zool.*, v. 6, 1927.

1107. **Ewart, J. C.**, and **Mitchell, J. C.** Lat. Sense Organs of Elasmobranchs. I. Laemargus. II. Common Skate Raja batis. *Tr. R.S. Edin.*, v. 37, 1891–95.

1108. **Ewart, J. C.**, and **Cole, F. J.** Dorsal Branches of Cranial and Spinal Nerves of Elasmobranchs. *Tr. Roy. Soc. Edin.*, v. 20, 1895.

1109. **Franz, V.** Nervensyst. d. Akranier. *Jena. Zeitschr.*, v. 59, 1923.

1110. **Ganfini, C.** Sviluppo d. s. n. simpatico n. ucelli. *Arch. Ital. d. Anat.*, 1916.

1111. **Garman, L.** Lat. Canal Syst. of Selachia and Holocephala. *Bull. Mus. Comp. Zool.*, v. 17, 1888.

1112. **Gaskell, W. H.** Involuntary Nervous System. London, 1916 (Bibl.).

1113. **Gast, R.** Entw. des Oculomotorius u. seiner Ganglien bei Selachier. *Mitth. Zool. Sta. Neapel*, v. 19, 1909.

1114. **Goette, A.** Entw. d. Kopfnerven b. Fischen u. Amphibien. *Arch. mikr. Anat.*, v. 85, 1914.

1115. **Goronowitsch, N.** Gehirn u. Cranialnerven v. Acipenser. *Morph. Jahrb.*, v. 13, 1888.

1116. —— Der Trigemino-facialis complex v. *Lota vulgaris*. *Gegenbaurs Festschr.*, v. 3, 1896.

1117. **Guthke, E.** Ganglien, etc., v. Torpedo. *Jena. Zeitschr.*, v. 42, 1907.

1118. **Harrison, R. G.** Histog. d. periph. Nervensyst. b. Salmo. *Arch. mikr. Anat.*, v. 57, 1901 ; *Biol. Bull.*, v. 2, 1901.

1119. **Held, H.** *Entw. des Nervengewebes b. d. Wirbeltieren.* Leipzig, 1909.

1120. **Herrick, C. J.** Cranial and First Spinal Nerves of Menidia. *J. Comp. Neur.*, v. 9, 1899.

1121. —— Doctrine of Nerve Components. *J. Comp. Neur.*, v. 14, 1904.

1122. **Heymans, J. F.**, and **Stricht, O. van d.** Syst. nerveux de l'Amphioxus. *Mém. Cour. Ac. Roy. Belgique*, v. 56, 1898.

1123. **Hill, C. J.** Enteric Plexuses. *Phil. Trans. R.S. London*, v. 215, 1927 (Bibl.).

1124. **His, W.**, Jr. Entw. d. Bauchsympathicus. *Arch. Anat. u. Phys.*, Abt. Anat., Suppl., 1897.

1125. **Huber, G. C.** Morph. of Sympathetic System, Folia Neuro-biol., v. 7, 1913 ; and Intern. Congress of Medicine, London, 1913.

1125a. **Johnson, S. E.** Sense Organs of Lat. Canal Syst. of Selachians. *J. Comp. Neur.*, v. 28, 1917.

1126. **Johnston, J. B.** Gehirn u. Cranialnerven der Anamnier. *Ergeb. Anat. u. Entw.*, v. 11, 1902.

1127. —— Cranial and Spinal Ganglia and Viscero-motor Roots in Amphioxus. *Biol. Bull.*, v. 9, 1905.

1128. —— Cranial Nerve Components of Petromyzon. *Morph. Jahrb.*, v. 34, 1905. Add. Notes on Cranial Nerves of Petromyzonts. *J. Comp. Neur.*, v. 18, 1908.

1129. —— Nervous Syst. of Vertebrates. London, 1908 (Bibl.).

1130. —— Central Nervous System of Vertebrates. *Ergeb. u. Fortschr. der Zoologie*, v. 2, 1910.

1131. **Julin, C.** Grand sympathique de l'Ammocoetes. *Anat. Anz.*, v. 2, 1887.

1132. **Kapers, C. A.** Der Geschmack, etc. *Psychiatr. neur. Bladen*, 1914.

1133. **Kingsbury, F.** Lateral Line System in American Amphibia and comparison in Dipnoans. *Tr. Am. Micr. Soc.*, v. 17, 1896.

1134. **Klinkhardt, W.** Beitr. z. Entw. d. Kopfganglien u. Sinneslinien der Selachier. *Jenaisch. Zeitschr.*, v. 40, 1905.

1135. **Knouff, H. W.** Origin of Cranial Ganglia of Rana. *J. Comp. Neur.*, v. 44, 1927.

1136. **Kohn, A.** Entw. d. symp. Nervensyst. d. Säugetiere. *Arch. mikr. Anat.*, v. 70, 1907.

1137. **Kuntz, A.** Devel. of Sympathetic (Mammals, Birds, and Fishes). *J. Comp. Neur.*, v. 20-21, 1910–11.

1138. —— Innervation of Digestive Tube. *J. Comp. Neur.*, v. 23, 1913.

1139. —— Devel. of Symp. Nerv. Syst. in Man. *Ibid.*, v. 32, 1920.

1140. **Kuntz, A.,** and **Batson, O. V.** Experim. Observations on Histogenesis of Sympathetic Trunks in Chick. *J. Comp. Neur.*, v. 32, 1920.

1141. **Kutchin, H. L.** Periph. Nervous Syst. of Amphioxus. *Proc. Am. Acad.*, v. 49, 1913.

1142. **Landacre, F. L.** Origin and Dist. of Taste-buds of Ameiurus. *J. Comp. Neur.*, v. 17, 1907.

1142a. —— Origin of Cranial Ganglia of Ameiurus. *J. Comp. Neur.*, v. 20, 1910.

1143. —— Epibr. Placodes of Lepidosteus. *J. Comp. Neur.*, v. 22, 1912.

1143a. —— Fate of Neural Crest in Urodeles. *Ibid.*, v. 33, 1921.

1144. **Langley, J. N.** Sympathetic System. Schaefer's *Text-book of Physiology*, v. 2, 1900. Autonomic Nervous System. Cambridge, 1921.

1145. **Locy, W. A.** On a Newly Recognised Nerve. *Anat. Anz.*, v. 26, 1905.

1146. **Malbranc, M.** Seitenlinie u. ihren Sinnesorgane bei Amphibien. *Z.W.Z.*, 26, 1875.

1147. **Merritt, O. A.** Theory of Components. *J. of Anat. and Phys.*, v. 39, 1904.

1148. **Mitrophanow, P.** Etude embryogénique sur les Sélaciens. *Arch. Zool. Exp. et Gén.*, S. 3, v. 1, 1893.

1149. **Müller, E.** Autonome Nervensystems b. Selachiern. *Arch. mikr. Anat.*, v. 94, 1920.

1150. —— Darmnervensystem. *Upsala Läk. förhandl.*, v. 26, 1921.

1151. **Müller, E.,** and **Ingvar, S.** Sympathicus b. d. Amphibien. *Upsala Läk. förh.*, v. 26, 1921.

1152. **Müller, E.,** and **Liljestrand, G.** Autonome Nervensyst. der Elasmobranchier, etc. *Arch. Anat. u. Phys.*, Abt. Anat., 1918.

1153. **Müller, L. R.** Lebensnerven. Berlin, 1924 (Bibl.).

1154. **Neumayer, L.** Histog. u. Morphog. d. periph. Nervensystems. Hertwig's *Handb. Entwickl.*, v. 2, 1906 (Bibl.).

1155. **Norris, H. W.** Cranial Nerves of Siren lacertina. *J. of Morph.*, v. 24, 1913.

1156. —— Branchial Nerve Homologies. *Zeit. f. Morph. u. Anthr.*, v. 24, 1924.

1157. —— Cranial Nerves of Certain Ganoid Fishes. *J. Comp. Neur.*, v. 39, 1925.

1158. **Norris, H. W.,** and **Hughes, S. P.** Nerves of Squalus acanthias. *J. Comp. Neur.*, v. 31, 1920.

1158a. —— Spiracular Sense Organ in Elasmobranchs, Ganoids, and Dipnoans. *Anat. Rec.*, v. 18, 1920.

1159. **Onodi, A.** Entw. d. symp. Nervensyst. *Arch. mikr. Anat.*, v. 26, 1885.

1160. **Parker, G. H.** Functions of Lat. Line Organs. *Bull. Bur. Fish.*, v. 24, 1904.

1161. **Pinkus, F.** Hirnnerven des Protopterus. *Morph. Arb.*, v. 4, 1895.
1162. **Platt, J. B.** Devel. of Periph. Nervous Syst. (Necturus). *Quart. J. Micr. Sci.*, v. 38, 1896.
1163. **Plessen, J. v.,** u. **Rabinovicz, J.** *Kopfnerven v. Salamandra.* 1891.
1164. **Pollard, H. B.** Lateral Line System of Siluroids. *Zool. Jahrb.*, Abt. Anat., 5, 1892.
1165. **Ranzi, S.** Organo di senso d. pr. placode epibr. d. Selaci. *Rend. Acad. Lincei Roma,* v. 1, 1925.
1166. **Rau, A. S.,** and **Johnson, P. H.** Devel. of Symp. n. s., etc., in Sparrows. *Proc. Zool. Soc. London,* 1923.
1167. **Reese, A. M.** Lateral Line System of Chimaera colliei. *J. Exp. Zool.,* v. 9, 1910.
1168. **Ridewood, W. G.** Spiracle, etc., in Elasmobranch Fishes *Anat. Anz.,* v. 11, 1896.
1169. **Rohde, E.** Nervensyst. v. Amphioxus. *Zool. Beitr.,* v. 2, 1888.
1170. **Ruge, G.** Gebiet d. Nervus facialis. *Festschr. C. Gegenbaur,* v. 3, Leipzig, 1897.
1171. **Ruud, G.** Hautsinnesorgane bei *Spinax niger. Zool. Jahrb.,* Abt. Anat., v. 41, 1920.
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1175. —— Origin of Nervus terminalis of Albino Rat. *J. Comp. Neur.,* v. 32, 1920.
1176. **Strong, O. S.** Cranial Nerves of Amphibia. *J. of Morph.,* v. 10, 1895.
1177. **Tretjakoff, D.** Skelett u. Muskulatur d. Flussneunauges. *Zeit. wiss. Zool.,* v. 128, 1926.
1178. —— Periph. Nervensystem d. Fl. *Ibid.,* v. 129, 1927.
1179. **Vitali, G.** Organo n. d. senso nell' orechio medio d. ucelli. *Intern. Monats. f. Anat. u. Physiol.,* 30, 1914.
1180. —— *Richerche di morfologia,* v. 3, 1923 ; v. 4, 1924.
1181. **Watkinson, G. B.** Cranial Nerves of Varanus. *Morph. Jahrb.,* v. 35, 1906.
1182. **Wijhe, J. W. van.** Nervus terminalis fr. Man to Amphioxus. *Verh. d. k. Ak. v. Wet. Amsterdam,* v. 21, 1918.
1183. —— Thymus, Spiracular Sense Organ, etc. *K. Akad. v. Wetensch. Amsterdam,* v. 26, 1923.
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1185. **Wilson, H. V.** Embryology of Sea Bass (Serranus). *Bull. U.S. Fish. Comm.,* v. 9, 1889.
1186. **Wright, R. R.** Hyomand. Cleft and Pseudobranchs of Lepidosteus and Amia. *J. Anat. and Physiol.,* v. 19, 1885.

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